

THE MIDDLE AMERICAN GENUS *ONYPTERYGIA* DEJEAN  
 (INSECTA: COLEOPTERA: CARABIDAE: PLATYNINI):  
 A TAXONOMIC REVISION OF THE SPECIES, WITH NOTES ABOUT  
 THEIR WAY OF LIFE AND GEOGRAPHICAL DISTRIBUTION

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ABSTRACT

Keys, descriptions, and illustrations distinguish the known species of the Middle American genus *Onypterygia* Dejean (type species *Onypterygia fulgens* Dejean), and each taxon is characterized in terms of structural features of adults, habitat, geographical distribution, and chorological affinities. For allopatric species that are markedly similar in structural features, a hypothesis of phylogenetic relationship is postulated. Fifteen new species are described.

The species of *Onypterygia* are arranged in seven groups, sequenced according to judgment about extent of departure from a generalized platynine body plan (type areas for new species in parentheses): *O. famini* group, including *O. famini* Solier and *O. cyanea* Chadoir; *O. wappesi* group, including *O. wappesi*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); *O. amecameca*, n. sp. (Mexico, state of México, Amecameca); *O. atoyac*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); *O. shpeleyi*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); and *O. pacifica*, n. sp. (Mexico, Oaxaca, Sierra de Miahuatlán); *O. aeneipennis* group, including *O. batesi*, n. sp. (Mexico, Tamaulipas, Sierra Madre Oriental [Sierra de Guatemala]), *O. aeneipennis* Chadoir, *O. cupricauda* Casey, *O. stenapteryx*, n. sp. (Mexico, Michoacán, Sierra Transvolcanica West), *O. pallidipes* Chadoir, and *O. rubida* Bates; the *O. perissostigma* group, including only *O. perissostigma*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), the *O. pusilla* group, including *O. pusilla* Chadoir and *O. rawlinsi*, n. sp. (Mexico, Nayarit, Sierra Transvolcanica West); the *O. angustata* group, including *O. longispinis* Bates, *O. angustata* Chevrolat, *O. pseudangustata*, n. sp. (Mexico, Puebla, Sierra Transvolcanic East), and *O. siblingi*, n. sp. (Mexico, Oaxaca, Sierra de Juárez); and *O. fulgens* group, including *O. iris* Chadoir, *O. championi* Bates, *O. donato* Ball and Shpeley, *O. chrysura* Bates, *O. kathleenae*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), *O. exeueros*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), *O. polytreta*, n. sp. (Panama, Chiriquí Province, Talamancan Cordillera, Cerro Pando), *O. crabilli*, n. sp. (Costa Rica, Puntarenas Province, Talamancan Cordillera, Monteverde), *O. quadrispinosa* Bates, *O. scintillans*, n. sp. (probably Costa Rica, Talamancan Cordillera), *O. fulgens* Dejean, *O. tricolor* Dejean, *O. hoepfneri* Dejean, and *O. sallei* Chadoir. New synonymy is as follows: *O. cyanea* Chadoir, 1878 = *O. valdestriata* Bates, 1884; *O. fulgens* Dejean, 1831 = *O. thoreyi* Mannerheim, 1844; *O. tricolor* Dejean, 1831 = *O. apicalis* Chadoir, 1837 = *O. tricolor* var. *dimidiata* Chevrolat, 1837. Other synonyms are as published by previous authors.

Geographical distribution of *Onypterygia* is analyzed in terms of altitudinal range, and nine areas of precinction, each of which is highland isolated by surrounding lowlands. The areas are, from south to north: Talamancan Cordillera; Chiapan-Guatemalan Highlands; Sierra Madre de Oaxaca; Sierra de Miahuatlán; Sierra de Atoyac; Sierra Transvolcanica East and West; Sierra Madre Oriental and Occidental. Seven areas have representatives of four to six species groups, but the northwesternmost (Sierra Madre Occidental) and southernmost (Talamancan Cordillera) have only two groups. At the species level, the northern centers (Sierra Madre Oriental and Occidental) lack precinctive species, but the southern Talamancan Cordillera has nine such species. Speciation, then, has been most frequent in the more southerly centers. Probably the northern centers have been invaded relatively recently, or evidence of older invasions has been lost because of extinctions.

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 Submitted 26 June 1995.

Speciation is postulated to have involved, during late Tertiary-Quaternary time, alternating sequences of geographical isolation (with consequent differentiation of the isolates) in the montane forested areas of precinction, followed by dispersals of previously isolated stocks. This explains both the extensive sympatry of the species groups (because of dispersal), and allopatry of species-level adelphotaxa (because of isolation and differentiation in different areas of precinction), although some speciation evidently has occurred within some of the areas of precinction (particularly the Sierra Transvolcanica West and the Talamancan Cordillera).

## INTRODUCTION

### *Prologue*

Adults of *Onypterygia hoepfneri* Dejean (Fig. 1) are spectacular beetles: large in size and brilliant green and maroon in color, they excite the aesthetic sensibilities and stimulate the acquisitive instinct of entomologists fortunate enough to locate them. In February 1966, Don Whitehead and I, during the year that we spent together in Mexico, obtained a large series of that species on the lower slopes of the Sierra Madre de Chiapas, to the north of Huixtla, in the state of Chiapas. We made this collection in a stand of oaks growing near the top of a mountain ridge. Concealed in bromeliads attached to the oak trees, the beetles were captured easily by detaching the plants and shaking them over a beating cloth laid on the ground.

Stimulated by the aesthetic appeal of these beetles and the wonder of the environment in which we found them, I think we knew then that *Onypterygia* would be high on the list of taxa for prompt study, following our eventual return to the University of Alberta. For personal reasons, I would have liked to do the revision, but we had agreed previously that the platynines were to be a major focus for Don's contribution to knowledge of the Mexican carabid fauna. In 1967 Don began the work while still a graduate student in Edmonton. He borrowed some supplementary material and, in 1968, studied the types of the species described by those great 19th-century entomologists, P. F. M. A. Dejean, M. de Chaudoir, and H. W. Bates.

Demands resulting from the need to complete his doctoral program interfered with study of *Onypterygia*. Other interruptions followed as the years drifted by. Periodically, I reminded him about this genus, and continued to send him material, including specimens that field parties from my department gathered, specimens sent to me for determination and as gifts, or that I came across in collections of institutions that I visited.

In 1987, Don returned to serious work on *Onypterygia*, and assembled a preliminary draft of a manuscript. The day-to-day requirements of his position in the Systematic Entomology Laboratory plus the time spent generously and willingly in helping others, deflected again the *Onypterygia* project, a deflection that was made permanent by terminal illness and death in May 1990.

I asked for and was granted the opportunity to complete the preparation of the manuscript for publication. Initially, I assumed that the manuscript was sufficiently complete that my task would involve only editorial work and assembly of the plates. A thorough review of the text and prepared figures revealed that much more was required. Because my contribution has been extensive, and because the text is quite different from that which I received, joint authorship seemed appropriate. Authorship confers credit for work done, but equally important, responsibility is established, also.

I am not sure that Don Whitehead would be pleased with the final product, but I am sure he would be relieved to have the task completed. Certainly, I enjoyed the work, for examining the specimens that we had collected brought back happy memories of our time together in the field. From time to time, though, my eyes misted with the thought that our association was a thing of the past. I was for-



Fig. 1.—Habitus, dorsal aspect, of *O. hoepfneri* Dejean. Male, total length 14.1 mm. Guatemala, Zacapa, 3 km SE La Union, 1400–1500 m (UASM).

tunate to have known Donald R. Whitehead and to have enjoyed his friendship for a period that seems all too brief.—George E. Ball

#### *History of Study*

The purpose of this paper is to provide a modern taxonomic treatment of the species of *Onypterygia*, as a contribution to the rapidly developing knowledge of

New World Platynini, thanks to the continuing efforts of Liebherr (1986, 1987, 1991a, 1991b, 1992), Moret (1989, 1990a, 1990b, 1993, 1994), and the late Georges Perrault (1990, 1991, 1992). The revision was begun by the senior author in the context of knowledge available at the time (summarized and augmented in part by Whitehead, 1973, 1974), before the individuals noted previously had undertaken their studies, and before Habu's (1978) classification provided a suitable background for genus-level revisions of the tribe Platynini.

Nearly all taxonomic work on *Onypterygia* was published during the 19th century. Although in use as a catalogue name, *Onypterygia* was described and validated first by Dejean (1831), who included three new Mexican species. The concept of the genus has remained essentially unchanged since then, and the name has been applied consistently except for an unjustified emendation as *Onychopterygia* by Agassiz (1847), which was used subsequently by several later authors, including Gemminger and Harold (1868:384), Chaudoir (1878), and Heyne (1895).

Subsequent investigation of Mexican carabid beetles led to description of one new species by Solier (1835:113), three by Chevrolat (1835:158–160), one by Chaudoir (1837:12), one by Castelnau (1840:42), one by Mannerheim (1844:869), and later, two more by Chaudoir (1863:225). These works were summarized by Gemminger and Harold (1868:384), who listed 12 described species.

The first revision of the genus was published by Chaudoir (1878), with description of four additional Mexican species, establishment of junior synonymy for three earlier names, and change to status of variety for another. Bates (1882: 130–133) extended geographical coverage of the genus through description of four new Central American species, as well as presentation of additional locality data for previously described taxa. In a supplement (1884:286–287), he described two additional Mexican species. Heyne (1895:25), evidently unaware of these important papers, validated the Hoepfner specific epithet *dimidiata* for a variety of *O. tricolor*. Casey (1920:224) described as new a species from Guerrero, Mexico. Finally, Ball and Shpeley (1992) described a new species of the genus from Costa Rica.

Casey's publication brought to 24 the total number of validly published species-group names, of which 19 were recognized as species and two as varieties. These names were listed by Csiki (1931:744) and Blackwelder (1944:37), both of whom credited the name *O. dimidiata* to Heyne and Taschenberg, rather than to Chevrolat (1835).

## MATERIALS AND METHODS

### Materials

This study is based on examination of more than 3000 adults of *Onypterygia*. Additionally, as a basis for comparison, the senior author examined in detail representatives of numerous Neotropical representatives of *Platynus* Bonelli and other platynine genera.

As noted in the Prologue, both authors contributed to the collection of much of the material on which this revision is based. The senior author contributed a manuscript that summarized his studies of type material and the historical background of study of the species, and provided a classification and descriptions of the included taxa, and preliminary phylogenetic and zoogeographic hypotheses for the included taxa. As well, he had prepared many illustrations of structural features. The junior author augmented these contributions by: inclusion of additional material not seen by the senior author; having the SEM figures prepared; adding more line drawings and maps; and assembling the plates.

Some of the additional specimens belonged to species that the senior author had recognized previously, based on single individuals, but declined to name, designating each instead by a lower-case

letter. Such additional specimens justified the senior author's judgment about species recognition. Some of the additional material represented four species (*O. donato* Ball and Whitehead; *O. shpeleyi*, n. sp.; *O. rawlinsi*, n. sp.; and *O. striblingi*, n. sp.) not seen by the senior author.

Most of the material studied by us is either in the Strickland Museum, Department of Entomology, University of Alberta (UASM), or in the U. S. National Museum of Natural History (USNM, T. L. Erwin, curator). Other collections housing types, or from which material was borrowed, are listed below, along with a four-letter coden used in the text to identify sources of specimens. The names of the respective curators are included, or for private collections, the names of the owners.

ACCS—Achille Casale Collection, Istituto di Zoologia dell' Università di Sassari, via Muroni 25, 07100 Sassari, Italy; AUEM—Entomological Museum, Department of Entomology, Auburn University, Auburn, Alabama 36849, USA (W. E. Clark); BMNH—Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom (N. E. Stork and M. J. D. Brendell); CASC—Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA (D. H. Kavanaugh); CDAE—California State Collection of Arthropods, Analysis and Identification Unit, California Department of Food and Agriculture, 1220 N Street, Sacramento, California 95814, USA (F. G. Andrews); CISC—California Insect Survey, Division of Entomology, University of California, Berkeley, California 94720, USA (J. A. Chemsak); CMNC—Entomology Division, Canada Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada (R. S. Anderson); CMNH—Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, USA (J. E. Rawlins, R. L. Davidson); CNCI—Canadian National Collection of Insects, Biological Resources Division, Centre for Land and Biological Resources Research, Agriculture Canada, K. W. Neatby Building, CEF, Ottawa, Ontario K1A 0C6, Canada. (Y. Bousquet); CUIC—Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999, USA (J. K. Liebherr); FFPC—Foster F. Purington Collection, Department of Entomology, Ohio State University, Columbus, Ohio 43210-1220, USA; FMNH—Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA (H. Dybas, R. L. Wenzel); FSCA—Florida State Collection of Arthropods, Division of Plant Industry, 1911 34th Street S.W., Gainesville, Florida 32602, USA (M. C. Thomas); INBC—Instituto Nacional de Biodiversidad, Apto. 22-3100, Santo Domingo de Heredia, 3100, Heredia, Costa Rica (Angel Solís); JEWC—J. E. Wappes Collection, J. E. Wappes, 5336 Fallen Oak, Oak Village North, Bulverde, Texas 78163, USA; MCPM—Milwaukee City Public Museum, 800 W. Wells Street, Milwaukee, Wisconsin 53233, USA (G. R. Noonan); MCZC—Department of Entomology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA (D. G. Furth); MNHP—Entomologie, Muséum National d'Histoire Naturelle, Paris 75005, France (T. Deuve); MSUC—Department of Entomology Collection, Michigan State University, East Lansing, Michigan 48824-1115, USA (F. W. Stehr); OXUM—Hope Entomological Collections, University Museum, Parks Road, Oxford OX1 3PW, United Kingdom (G. McGavin); RHTC—Robert H. Turnbow Collection, R. H. Turnbow, Jr., Directorate of Engineering and Housing, Building 1404, Fort Rucker, Alabama 36362-5137, USA; SEMC—Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044, USA (J. S. Ashe); TAMU—Department of Entomology Insect Collection, Department of Entomology, Texas A & M University, College Station, Texas 77843, USA (H. R. Burke); UCDC—The Bohart Museum of Entomology, University of California, Davis, California 95616, USA (R. M. Bohart); UMMZ—Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, USA (M. F. O'Brien); UNAM—Colección Entomología, Instituto Biología, Universidad Nacional Autónoma de México, Apartado Postal 70133, 04510 México D. F. (M. and C. Santiago Zaragoza); UNAN—Entomological Collection, Escuela de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de Nicaragua, Leon, Nicaragua (J. M. Maes); ZSMC—Zoologische Staatsammlung, Munchhausenstraße 21, D-81247, München, Germany (M. Baehr; G. Scherer).

Holotypes and allotypes of newly described taxa have been deposited in the U. S. National Museum of Natural History, or returned to the appropriate lending institutions.

## Methods

### Taxonomic Conventions

Taxonomic principles, criteria for ranking groups of specimens as species, and general working methods are standard, and have been explained previously (see, for example, Ball and Negre, 1972, and Whitehead, 1972). The senior author chose not to use the subspecies category, in the spirit that it is much more important to recognize how geographically differentiated organisms fit together than it is to distinguish them nomenclaturally. However, subspecies names are used as a convenient informal notation to discuss geographical variation in the species *O. fulgens* and *O. tricolor*.

We use only one informal category (species group) between genus and species. For the present, this seems adequate to express our understanding of the evolutionary structure of the genus.

#### *Phylogenetic Considerations*

The species groups are based on a combination of more or less distinctive features, and each group is postulated as monophyletic. Within species groups, close phylogenetic relations are postulated for allopatric or parapatric species pairs, where marked similarities in distinctive features seem decisive.

Species groups are in the sequence that reflect the views of the senior author about degree of primitiveness, beginning with the *famini* group, and ending with the *fulgens* complex of the *fulgens* group.

Terms for phylogenetic analysis are standard, except for "adelphotaxon." This word was introduced by Ax (1987:36) as a substitute for "sister taxon." The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages.

#### *Taxonomic Treatments of Species*

These include the standard elements of: synonymy; a diagnosis; figures of male genitalia for most species; a brief description of each species, including measurements; notes about habitat and plant community occupied, as inferred from collecting data; and a statement about geographical range, which is amplified by a range map for each species. Additionally, we include statements about chorological affinities (stated in terms of range overlap with other species of the genus, particularly close relatives), and postulated phylogenetic relationships. The latter two aspects are as much properties of a species as are its structural features, and should be included, therefore, in a taxonomic treatment.

#### *Measurements*

These were used to indicate size and proportions. The following measurements were made, using an ocular micrometer in a Wild S5 Stereobinocular Microscope, at a magnification of 25 $\times$ : length of head—linear distance from anterolateral angle of clypeus to posterior margin of left eye (if the left side was damaged, the measurement was taken on the right side); length of pronotum—linear distance from anterior (apical) to posterior (basal) margin, measured along the midline; width of pronotum—greatest linear transverse distance, measured at right angle to the midline; width of pronotum at base—linear distance between posterolateral angles; length of elytra—linear distance from basal ridge to apex of one elytron, along the suture; width of elytra—greatest linear transverse distance across both elytra, measured at right angle to suture.

These measurements were added or combined in ratios, and designated as follows: TL—body length (sum of length of head, pronotum, and elytra); PL/PW—length of pronotum/width of pronotum; WP/WH—maximum width of pronotum/width of head; LP/WP—length of pronotum/maximum width of pronotum; WP/WPb—maximum width of pronotum/width of pronotum at base; and LE/WE—length of elytra/width of elytra.

In the descriptions, qualitative terms are offered to designate three classes, and thus to generalize the numerical values: for size (TL), small, intermediate, and large; for ratios, low, intermediate, and high. Each class represents approximately a third of the measured range of variation of each measurement and ratio.

#### *Dissections and Illustrations*

Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine, in microvials, pinned beneath the specimens from which the sclerites had been removed. Hind wings, and sclerites that had been gold-coated for study with the scanning electron microscope were glued to cards and pinned beneath the specimens from which they had been removed.

A Cambridge S-250 scanning electron microscope was used to examine and photograph gold-coated sclerites. Line drawings were prepared by using a camera lucida (drawing tube) attached to a Wild S5 stereobinocular microscope.

#### *Descriptions*

Descriptive statements are consolidated to reduce redundancy: those statements that apply to all species of *Onypterygia* are in the generic description, and are not repeated elsewhere; distinctive character states of all species of a group are in the group treatment; and character states confined to individual species appear in the specific descriptions. The disadvantage to this method of presentation is that, to obtain a full description of a species, one must read the three descriptions: specific, species group, and generic.

### Type Material

For type specimens (holotypes, lectotypes, allotypes, and paratypes), label data are reproduced as exactly as possible, short of photographic images. This includes information about label shape (if other than square or rectangular), color of paper (other than white), color of ink (other than black), and nature of script (handwriting, rather than printing). Words referring to these properties are placed in square brackets to distinguish them from the text of the labels. Each label begins and ends with quotation marks; line endings are indicated by slash marks (/).

### Catalogue Citations of Species

Catalogue entries noted in the synonymy of the genus *Onypterygia* (Csiki, 1931:743–744; Blackwelder, 1944:47) are not repeated in the species' synonymies.

### Terms for Structural Features

Most of the words we used to designate details of structures are found in entomology textbooks or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use, although they have been used by the junior author in several publications (e.g., Shpeley and Ball, 1994). We provide information about these words here. Also, we draw attention to some special features of adults useful in species recognition.

**Body Parts.**—The term "segment" is restricted to those body parts that reflect embryonic somites; thus, somite-like portions of the abdomen are referred to as segments.

Abdominal segments are designated by Roman numerals, corresponding to the respective somites. The first complete sternum is III, and the last one normally exposed is VII. For numbering of the genitalic segments, we follow Bils (1976).

Portions of limbs are designated by the suffix "-mere," the prefix depending upon the limb in question: antenno-, palpo-, tarso-, etc.

**Microsculpture.**—A sculpticell is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculpture (Allen and Ball, 1980:486). Surface sculpture of the elytra provides some taxonomically useful features (Fig. 2–5). For most species, microlines are very fine; the transverse lines persist, while most of the longitudinally-oriented lines are absent, or almost so (Fig. 2, 4A, 5A), except in foveae (Fig. 4C, 5C). For *O. hoepfneri*, both transverse and longitudinally directed lines are about equally distinct.

Mesh pattern ranges from nearly isodiametric (mesh length/width ca. 1.00; Fig. 2) to slightly transverse (mesh L/W more than 1.00; Fig. 3). Table 1 summarizes measurements and shows that mesh size and shape are not correlated simply with size of elytra. For example, the *O. wappesi* specimen is substantially smaller than the specimen of *O. hoepfneri*, but the meshes of the former are longer than the meshes of the latter. Also, the elytra of *O. iris* Chaudoir and of *O. hoepfneri* are the same size, but the meshes of the former are wider than the meshes of the latter.

**Macrosculpture and Punctures.**—The integument of adults of most species of *Onypterygia* is smooth overall. Some species have a preapical lateral swelling on each elytron (a callus; Fig. 11B: pc). Foveae are evident on the elytral disc and apical declivity of two species (Fig. 5B, 43).

**Antennae.**—In descriptions of color, two parts are referred to: basal (antennomeres 1–4), and apical (antennomeres 5–11).

**Labium.**—The word "ligula" is used for glossae + paraglossae. In turn, the fused, sclerotized glossae characteristic of beetles are termed the glossal sclerite (Ball and Shpeley, 1983:746).

**Elytra.**—Longitudinal grooves on the dorsal surface ("striae" of most authors) are designated as interneurs (Erwin, 1974:3–5). For a different perspective on the use of this term, see Cooper (1990).

**Tarsi.**—The term climbing setae is used by Stork (1980:177) to designate "normal adhesive setae." Located on the ventral surfaces of tarsomeres 1–4, these setae are of the "simple type" exhibiting few morphological adaptations for adhesion (Stork, 1980:305). In *Onypterygia* adults (Fig. 11D:cs), as in adults of *Demetrias atricapillus* Linnaeus (Stork, 1980:195), the climbing setae are round in cross section, but slightly flattened dorsoventrally, and curved proximally preapically.

**Male Genitalia.**—In form and range of variation of the male genitalia (median lobe, parameres, and internal sac), *Onypterygia* does not differ much from the related genus, *Platynus* (cf. Liebherr, 1987: 318, fig. 57; 339, fig. 75–77; 349, fig. 84–88). The internal sac exhibits striking modification, from asetose to setose, with fields of setiform spines (Fig. 25C, D), or much of the ventral surface with short setiform spines. Spinose sclerites (Fig. 44D:Sc1, Sc2) and lobes with microtrichia basally and apically (Fig. 48, 80) characterize many species.

**Ovipositor.**—Ball and Shpeley (1983:746) explain terms used for sclerites and setae, and for orientation of sclerites. Note that for stylomeres, the surfaces that are ventral in the infolded or retracted position are lateral in the extended position; such surfaces are designated as lateral.

Stylomere 2 (Fig. 12–16) of *Onypterygia* females provides useful diagnostic features, the most

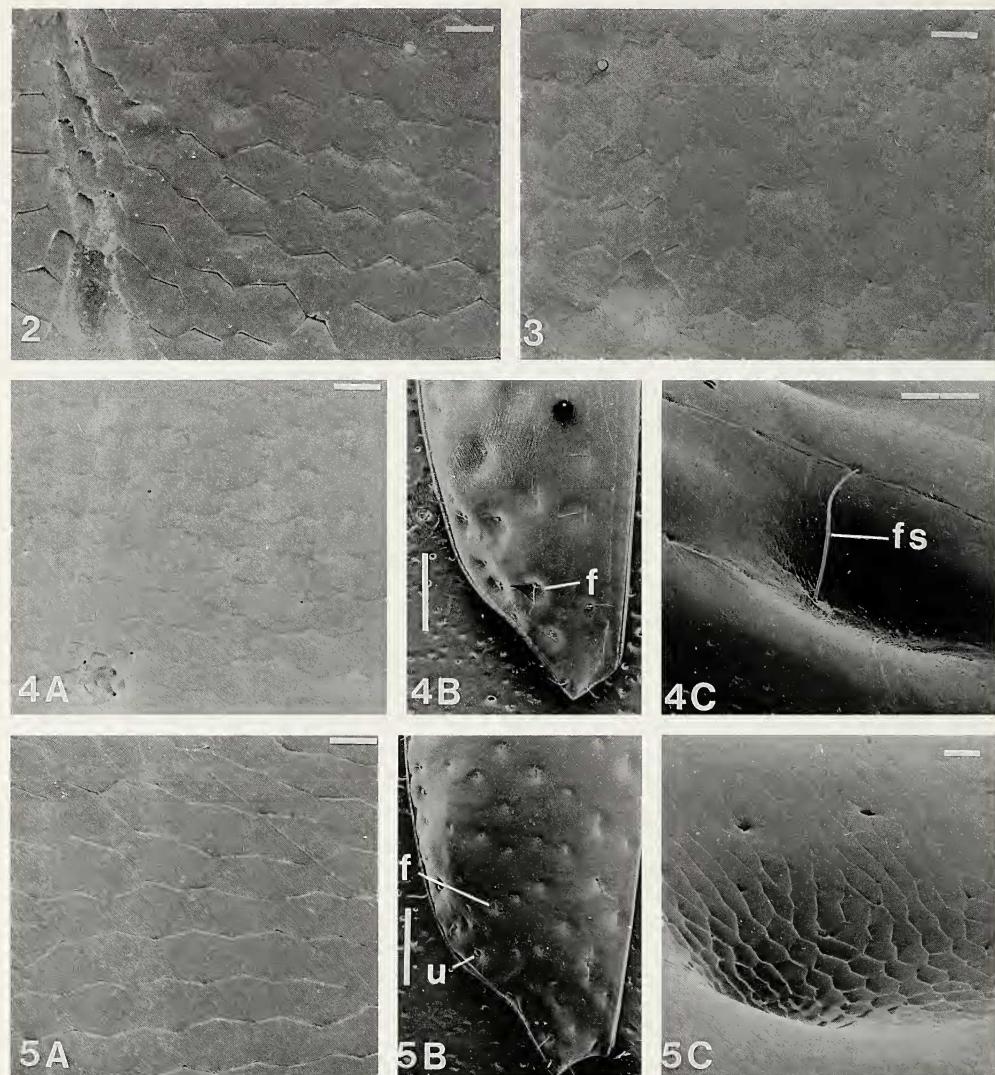


Fig. 2-5.—SEM photographs of dorsal surfaces of elytra. Fig. 2, 3. Microsculpture of elytral disc, in basal third, interval 3, of: 2, *O. famini* Solier; 3, *O. hoepfneri* Dejean. Fig. 4, 5. Elytra: A—microsculpture of elytral disc, in basal third, interval 3; B—apical portion of elytron, showing foveate punctures on disc and apical declivity; and C—foveate punctures, enlarged, of: 4, *O. polytreta*, n. sp.; and 5, *O. crabilli*, n. sp. Legend: f—foveate puncture, fs—seta in foveate puncture, u—umbilicate puncture. Scale bars: for Fig. 2-4A, 5A, 5C = 10  $\mu\text{m}$ ; for Fig. 4C = 100  $\mu\text{m}$ ; for Fig. 4B, 5B = 1.0 mm.

striking being the dense pad of ensiform setae on the lateral surface (Fig. 16A; cf. Fig. 12A:es) that characterizes some species.

#### TAXONOMIC ACCOUNTS

##### Genus *Onypterygia* Dejean

*Onypterygia* Dejean, 1831:346. Species originally included: *O. fulgens* Dejean, *O. hoepfneri* Dejean, and *O. tricolor* Dejean. Type species: *O. fulgens* Dejean (designated by Hope, 1838:72); Castel-

Table 1.—Measurements and proportions of microsculpture mesh of a sample of *Onypterygia* adults.

Species	Sculpticell L/W		Sculpticell width ( $\mu$ )		Elytron width (mm)
	Range	Mean	Range	Mean	
<i>O. wappesi</i>	0.78–0.94	0.84	13.60–15.30	13.94	1.99
<i>O. shpeleyi</i>	0.25–0.35	0.30	20.00–23.00	21.40	1.60
<i>O. famini</i>	0.80–1.00	0.90	13.60–17.00	15.30	2.08
<i>O. iris</i>	0.70–1.00	0.94	13.60–17.00	14.45	3.15
<i>O. polytreta</i>	0.57–0.70	0.61	15.30–18.70	17.34	2.90
<i>O. crabilli</i>	0.54–0.70	0.66	17.00–20.40	18.02	2.74
<i>O. hoepfneri</i>	1.38–1.92	1.59	10.20–11.90	10.88	3.15

nau, 1840:41; Chevrolat, 1847:117; Chenu and Desmarest, 1851:135; Lacordaire, 1854:358; Bates, 1882:130; Casey, 1920:224; Csiki, 1931:743; Blackwelder, 1944:37; Whitehead, 1973:175; Whitehead and Ball, 1975:595; Erwin et al., 1977:4.31; Reichardt, 1977:413; Liebherr, 1986:22, 86; Ball and Shpeley, 1992:403; Liebherr, 1992:6.

*Onychopterygia* Agassiz, 1847:260 (unjustified emendation). Gemminger and Harold, 1868:384; Chaudoir, 1878 (1879):275.

#### Generic Name

*Onypterygia* is based on two Greek words: *onyx*, claw; and *pterygion*, little wing, or feathers. Together, the words would seem to mean “feathered claws,” in allusion to the strikingly developed pectinations on the claws of adults of this genus (Fig. 11E–H).

#### Diagnostic Combination

With character states of subtribe Platynina (Habu, 1978:4), and tarsomere 4 of fore tarsus asymmetrically lobate apically (Fig. 11C:l-4) tarsal claws pectinate, pectinations curved ventromesally, long (Fig. 11E–H), head slightly constricted behind eyes and across occiput, and median lobe of male genitalia pale in color, not melanistic. The long, curved pectinations of the tarsal claws are virtually sufficient in themselves to distinguish *Onypterygia* adults from those of other platynine genera.

#### Description

With character states of subtribe Platynina. Habitus (Fig. 1, 17–20) slender, body terete, elytra elongate. Length (TL) ca. 5–18 mm, width ca. 2–7 mm. Range of values in Table 2 for following ratios: WP/WH, LP/WP, WP/WPb, and LE/WE.

**Color.**—Body and elytra rufous to blue, maroon, and green, alone or in combination. Antennae, mouthparts, and legs piceous to rufotestaceous.

**Microsculpture.**—Ventral surface with mesh pattern generally transverse. Head dorsally with mi-

Table 2.—Range of variation in measurements (mm) and values for selected ratios for species groups of the genus *Onypterygia* Dejean.

Species group	TL (mm)	WE (mm)	WP/WH	LP/WP	WP/WPb	LE/WE
<i>perissostigma</i>	8.2	2.5	1.04	1.16	1.16	1.96
<i>wappesi</i>	5.4–8.0	2.2–3.5	1.41–1.56	0.78–0.88	1.20–1.40	1.42–1.55
<i>aeneipennis</i>	6.7–8.7	2.7–3.3	1.28–1.39	0.84–0.91	1.22–1.28	1.47–1.60
<i>famini</i>	9.0–11.5	3.4–4.4	1.31–1.38	0.90–0.92	1.17–1.20	1.53–1.65
<i>pusilla</i>	7.0–9.0	2.7–2.9	1.33	1.18	1.29	2.00
<i>angustata</i>	7.5–11.3	3.0–4.0	1.33–1.56	0.84–1.00	1.18–1.25	1.73–1.77
<i>fulgens</i>	10.4–17.5	3.8–6.4	1.16–1.55	0.75–1.16	1.19–1.47	1.70–2.05

crolines distinctly impressed to absent (surface smooth), mesh pattern isodiametric to slightly transverse. Labrum with mesh pattern isodiametric to slightly transverse in places, microlines distinctly impressed, sculpticells slightly convex. Pronotum with microlines distinctly impressed to evanescent to absent (surface smooth); mesh pattern transverse. Elytra (Fig. 2, 3, 4A, 5A) with microlines distinctly impressed to evanescent to absent in part or entirely (surface smooth); mesh pattern isodiametric (Fig. 2) to transverse (slightly, Fig. 4A, 5A; and markedly), to slightly elongate (Fig. 3).

**Luster.**—Surface dull to shining, to slightly iridescent.

**Macrosculpture.**—Surface generally smooth. Head with shallow frontal impressions, linear or in form of irregular basins. Vertex between eyes without or with distinct ridge each side. Elytra smooth except more or less impressed interneurs, or with prominent foveae (Fig. 4B, C; 5B, C; 20); or with more or less distinctly developed lateral preapical callus (Fig. 11B:pc). Abdominal sterna II–VII laterally with surface irregularly sculptured by depressions of various sizes.

**Chaetotaxy (Fixed Setae).**—Array standard for Platynina, with exceptions: medial pair of lateral setae of pronotum present or absent; each elytron with three or two discal setae (anterior seta present or absent). Setal formula of legs as follows (numbers in sequence fore, mid, hind): coxae (0–2–2); trochanters (1–1–1); femora, ventrad (2–2–2 or 2–2–3), dorsally (ca. 10–ca. 10–0 to 2). Tarsomere 5 (Fig. 11D, G:vs) with row of setae on each ventrolateral margin. Abdominal sterna IV–VI each with single pair or more of ambulatory setae. Abdominal sternum VII with setae near posterior margin: one or two pairs in males, two to seven pairs (14 setae) in females.

**Head.**—Average for Platynina: clypeus rectangular, transverse. Occiput behind eyes slightly constricted, marked dorsally by shallow transverse depression. Eyes slightly flattened to markedly convex, prominent. Antennae average for Platynina: antennomeres 1–3 with few apical setae; antennomeres 4–11 with dense vestiture of short and varied sense organs; antennomeres slender, longer than wide.

**Mouthparts.**—Average for Platynina. Mandibles as in Fig. 6A–F. (See Acorn and Ball, 1991, for explanation of structural details.) Palpomeres with terminal articles slender, elongate. Mentum with prominent tooth.

**Prothorax.**—Pronotum transverse (Fig. 21, 22) to longer than wide (Fig. 47), dorsal surface slightly convex. Anterior and posterior margin each with groove more or less clearly developed, and thus more or less clearly beaded; lateral margins beaded partially or completely, or not beaded. Median longitudinal impression distinct but shallow; anterior transverse impression distinct to evanescent; posterolateral impressions basin-like to linear, co-extensive or not with lateral marginal grooves. Anterior (or apical) margin straight (Fig. 47) to slightly concave (Fig. 39, 54A); lateral margins rounded, evenly so posteriorly (Fig. 28, 73) or sinuate (Fig. 21, 22, 38); posterior (or basal) margin straight (Fig. 21, 53), slightly convex (Fig. 22, 69), or markedly convex (Fig. 30B), sinuate laterally (Fig. 67). Anterolateral angles narrowly rounded, projected forward slightly, or not. Posterolateral angles acute (Fig. 21), rectangular (Fig. 22), to broadly rounded (Fig. 28, 73). Prosternum with apex of intercoxal projection rounded or truncate.

**Pterothorax.**—Average for Platynina: metathorax of normal proportions, with metepisterna longer than wide at base; or short, with anterior and lateral margins nearly equal, i.e., metepisternum about as long as wide.

**Elytra.**—Elongate, each elytron from about 1.5 to about twice as long as wide; humeri fully developed and broadly rounded, or obliquely narrowed; lateral margins straight, slightly sinuate medially or broadly rounded, and narrowed and more or less sinuate preapically (Fig. 4B, 5B, 7, 8); apex rounded (Fig. 7, 8), or projected as spine of varying length (Fig. 4B, [denticulate], 5B, 10 [acuminate, spine short], 11A:ae [acuminate, spine long]); apex of suture rounded or variously denticulate and projected (Fig. 8:se). Basal groove and ridge distinct, complete. Intervals flat; interneurs variously developed, from all interneurs impressed equally throughout their length (Fig. 7, 8) to only interneur 1 distinctly impressed, others much shallower, especially on apical declivity (Fig. 10:I1, I2; 11A); parascutellar interneur separate from interneur 1.

**Hind Wings.**—Macropterous or brachypterous, or dimorphic. Fully developed wings with oblongum and wedge cells (Fig. 23, 78, 79:o, w) complete.

**Legs.**—Long and slender. Mid- and hind tibiae each with three rows of spines, dorsal (or posterior) surface not spined. Hind tarsomeres 1–3 each bisulcate or not; tarsomere 4 bilobed (Fig. 11C:I-4), lobes slightly asymmetric, ventrally moderately (Fig. 11C) to densely (Fig. 11F) setose or ciliate. Setae of climbing type. Claws virtually “chelate” (see Liebherr, 1986:26) with long pectinations (Fig. 11D–H:p) curved ventromesally. Males with biseriate adhesive vestiture on fore tarsomeres 1–4 (cf. Stork, 1980:190, fig. 9E–H; 10A–C; 17C, D).

**Abdomen–Pregenital Segments.**—Sterna II–VII average for Platynina (macrosculpture and chaetotaxy noted above).

**Male Genitalia.**—Median lobe slender, elongate, in lateral aspect curved ventrad (Fig. 32A, 59A); anopic (i.e., membranous portion dorsal, and extended about half length of median lobe); apical portion

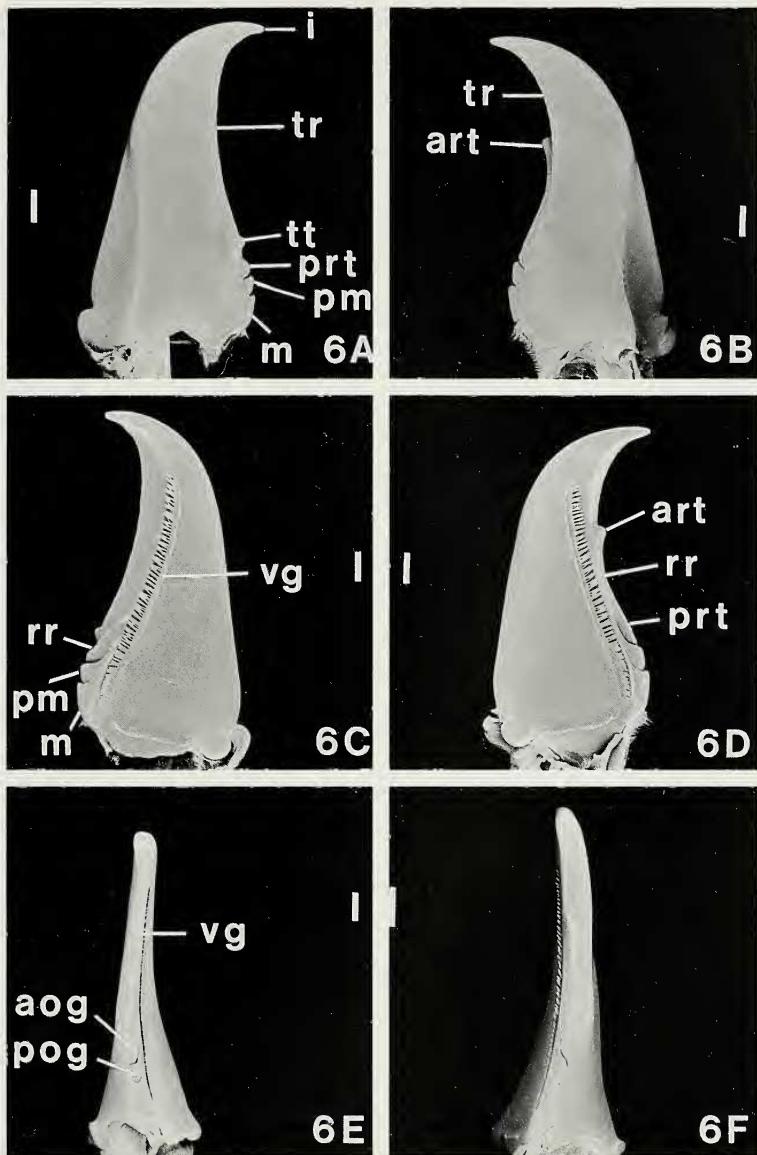


Fig. 6.—SEM photographs of mandibles of *O. famini* Solier. A, C, E. Left mandible: dorsal, ventral, and occlusal aspects, respectively. B, D, F. Right mandible: dorsal, ventral, and occlusal aspects, respectively. Legend: aog—anterior occlusal groove, art—anterior retinacular tooth, i—incisor tooth, m—molar tooth, pm—premolar tooth, pog—posterior occlusal groove, prt—posterior retinacular tooth, rr—retinacular ridge, tr—terebrial ridge, tt—ventral groove. Scale bars = 100  $\mu\text{m}$ .

very short (Fig. 44C, D), to moderately long (Fig. 89); in dorsal aspect, apex acute (Fig. 44A) to more broadly rounded (Fig. 56A), to spatulate (Fig. 82A). Parameres (Fig. 59A) average for Platynina, left larger than right, both quite broad, paddle-like, each with apex broadly rounded, asetose.

Internal sac short (Fig. 32A) or markedly elongate (Fig. 97A, B), with or without basal and preapical lobes. Armature microtrichial patches, or patches of spinose sclerites (Fig. 44D:Sc1, Sc2), or of setose spines (Fig. 25C, D:s.sp; 82C), or generally covered with short setose spines (Fig. 31C).

**Ovipositor.**—Valvifers average for Platynina. Styломere 1 with row of setae preapically. Styломere

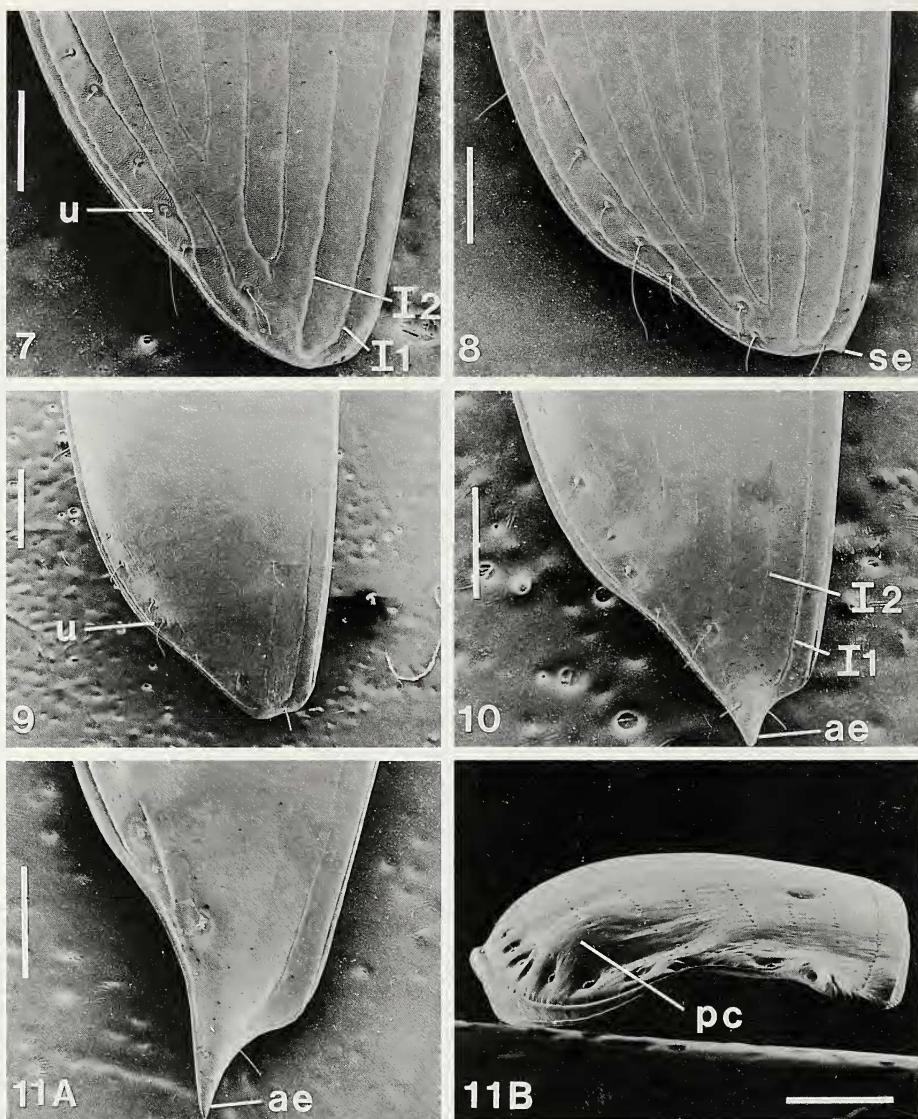


Fig. 7–11B.—Left elytron, apical portion, dorsal aspect, of: 7, *O. famini* Solier; 8, *O. wappesi*, n. sp.; 9, *O. hoepfneri* Dejean; 10, *O. longispinis* Bates; 11A, *O. kathleenae*, n. sp.; 11B, left elytron, postero-dorsal aspect of *O. kathleenae*, n. sp. Legend: ae—apical spine of elytron, I1—interneur 1 or sutural interneur, I2—interneur 2, pc—preapical callus, se—sutural denticle of elytron, u—umbilical puncture. Scale bars: for Fig. 7, 8, 10, 11A, 11B = 500 µm; for Fig. 9 = 1.0 mm.

2 with standard array of setae (Fig. 12–16:s2): lateral and medial ensiform setae (es, mes), pair of nematiform setae ventrally (ns) and six to ten pegs in sensory groove (sg). Three forms, as follows: form 1, ventral surface narrow, dorsal surface markedly curved, with lateral ensiform setae more or less marginal, and with single medial ensiform seta (Fig. 12A, B; 14); form 2, broad, dorsal surface less curved, ensiform setae numerous, remote from dorsal margin, and medial ensiform seta present (Fig. 15A, B); and form 3 as in form 2, but broader, lateral ensiform setae remote from dorsal margin, clustered as pad, and medial ensiform seta absent (Fig. 16A, B).

*Internal Female Genitalia*.—Investigated in two species only. For *O. famini*, bursa copulatrix bul-

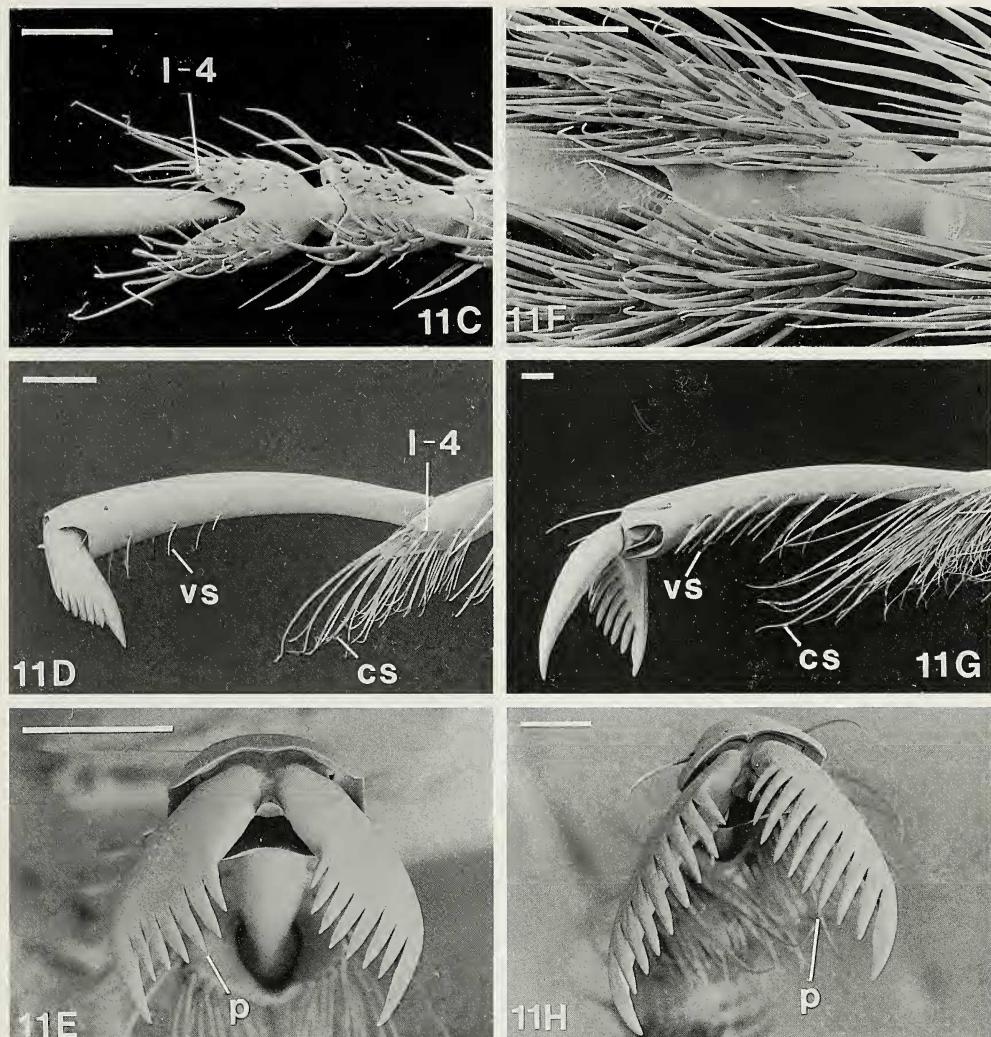


Fig. 11C–H.—SEM photographs of left hind tarsomeres of *Onypterygia* species. C–E, *O. perisostigma*, n. sp.: C, apical portion of 2, 3, and 4, and basal portion of 5, ventral aspect, 3 and 4 with climbing setae in lateral rows; D, apical portion of 4, with climbing setae ventrally, and 5, with claws and ventrolateral setae, lateral aspect, 4, with climbing setae ventrally; E, claws, terminal aspect. F–H, *O. fulgens* Dejean: F, apical portion of 3, 4, and basal portion of 5, 3 and 4 with climbing setae in dense lateral rows; G, apical portion of 4, with ventral climbing setae, and 5, with claws and ventrolateral setae, lateral aspect; H, tarsal claws, terminal aspect. Legend: cs—climbing seta, I-4—terminal lobe of tarsomere 4, p—pecten of tarsal claw, vs—ventrolateral seta of tarsomere 5. Scale bars = 100  $\mu\text{m}$ .

bous, about as wide as long, and basal half slightly sclerotized; spermatheca digitate, short, annular, on short duct; spermathecal gland duct inserted at base of spermatheca, with large apical bulb constricted at base.

For *O. fulgens*, bursa copulatrix ca. four times longer than wide, folded, accordion-like, with surface sclerotization confined to base; spermatheca and spermathecal gland as described for *O. famini*, above (cf. Liebherr, 1986:13, fig. 5C, *O. tricolor* Dejean).

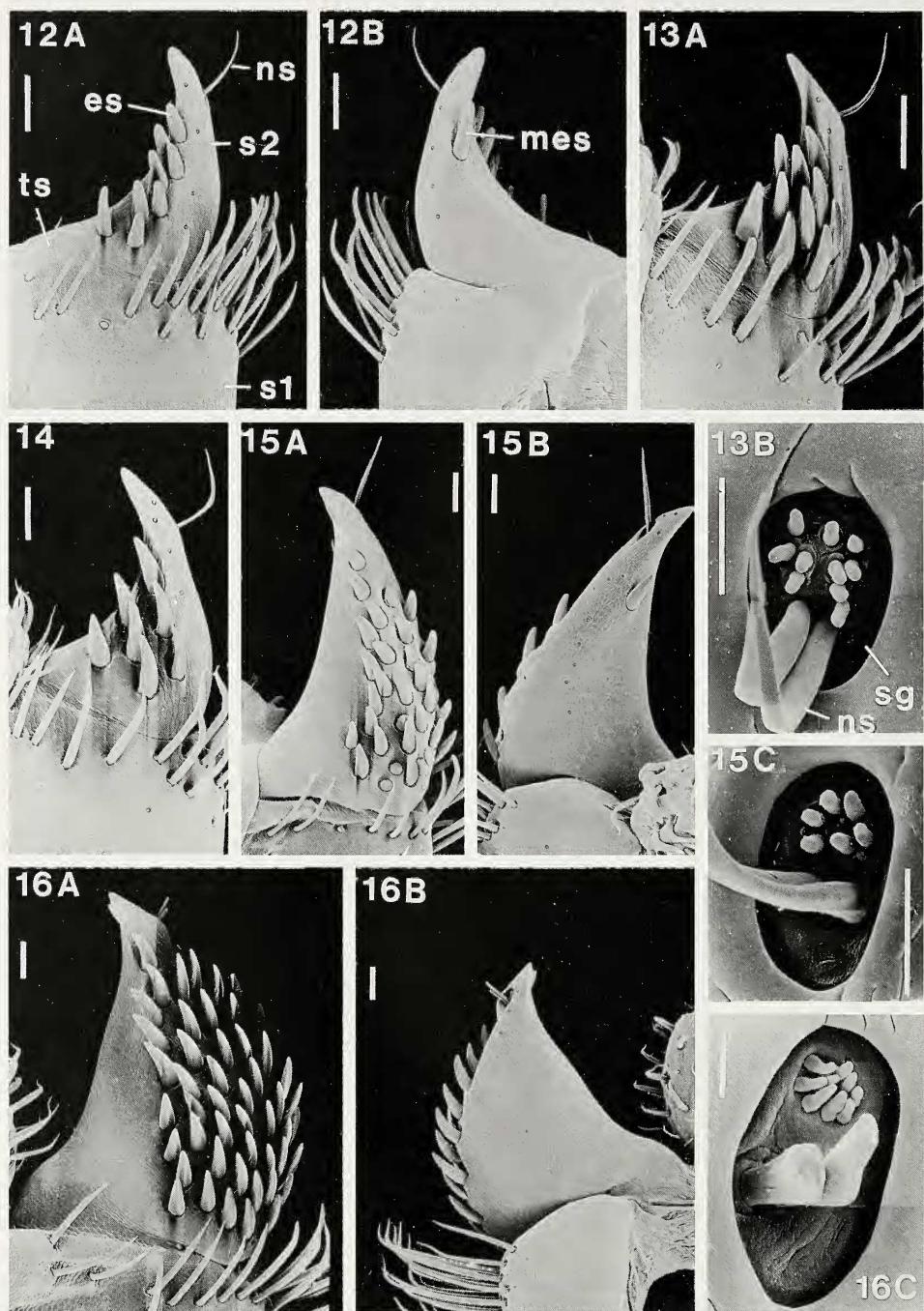


Fig. 12–16.—SEM photographs of left stylomeres of ovipositors of *Onypterygia* species. Fig. 12, stylomere 2 and apical portion of stylomere 1, of *O. wappesi*, n. sp.: A, lateral aspect; B, medial aspect. Fig. 13, stylomere 2 and apical portion of stylomere 1 of *O. batesi*, n. sp.: A, left lateral aspect; B, ventral aspect, showing sensory furrow with two nematiform setae and ten sensory furrow pegs. Fig. 14, stylomere 2 and apical portion of stylomere 1, lateral aspect, of *O. cupricauda* Casey. Fig.

### Geographical Distribution

The range of *Onypterygia* extends from Nearctic northern Mexico through Neotropical Middle America to northern South America.

### Way of Life

Adults of most species of *Onypterygia* are arboreal, collected commonly by beating vegetation (both trees and shrubs, and leaf litter that accumulates in tangles of vines and branches of standing plants), although some have also been found on the ground. They fly readily during the day, when disturbed. Many specimens have been collected at night, principally by ultraviolet light traps; thus, they seem to be night-active. During the dry season, especially January through April, apparently they become inactive, but may be found in abundance in the leaf axils of arboreal bromeliads. The genus is forest-inhabiting, ranging from rather dry lowland woodlands to middle montane cloud forests. Characteristic of moderate altitudes in Middle American forests, *Onypterygia* tends to be replaced ecologically by various Lebiini in the lowlands, and to be limited in uplands by the occurrence there of colder, drier circumstances. Because of these limiting factors, many species are quite widespread, yet exhibit complex patterns of geographical variation.

### Relationships

Dejean (1831:277–279) placed *Onypterygia* in the Truncatipennes (second subtribe, characterized by lack of a constricted head), near the lebiine genera *Demetrias* and *Dromius*, on the basis of: body more or less elongate and palpi not securiform; then, separated from the other two genera by claws of the tarsi with very pronounced denticles. Dejean noted the resemblance between *Dyscolus* and *Onypterygia*, and further with additional platynine genera: *Dolichus*, *Platynus*, and *Anchomenus*. He suggested that *Onypterygia* may be intermediate between the Feroniens (to which the above-noted genera belonged) and the Truncatipennes. Hope (1838:73) suggested that *Onypterygia* should be placed in a distinct “family” (i.e., tribe). Castelnau (1840:41), following Dejean, included *Onypterygia* in the tribal group Lebiites, one of the major truncatipennian elements.

Chenu and Desmarest (1851) placed *Onypterygia* in the tribe Simplicimanæ (second division, Calathides), on the basis of the pectinate tarsal claws, and other platynine features. Lacordaire (1854:358) placed *Onypterygia* in “Tribu XXXV, Anchomenides,” the approximate equivalent of the modern group Platynini. He noted the truncatipennian affinities that concerned his predecessors, but the close overall resemblance between *Onypterygia* and the genus *Dyscolus*, concluding that the former genus formed a transition between the Truncatipennes and the Anchomenini. Chaudoir (1878) did not comment about relationships of *Onypterygia*, but treated it in the same work with the platynine genera *Dicranoncus* Chaudoir and *Colpodes* MacLeay. Subsequent authors have included *Onypterygia*

15, stylomere 2 and apical portion of stylomere 1, of *O. exeuross*, n. sp.: A, lateral aspect; B, medial aspect; C, ventral aspect, showing sensory furrow with two nematiform setae and six sensory furrow pegs. Fig. 16, stylomere 2 and apical portion of stylomere 1, of *O. sallei* Chaudoir: A, lateral aspect; B, medial aspect; C, ventral aspect, showing sensory furrow with bases of two nematiform setae and nine sensory furrow pegs. Legend: es—ensiform seta, mes—medial ensiform seta, ns—nematiform seta, ts—trichoid seta, S1—stylomere 1, S2—stylomere 2, sg—sensory furrow, sgp—sensory furrow peg. Scale bars: for Fig. 13A, 15C, 16C = 10 µm; for Fig. 12A–13A, 14–15B, 16A–16B = 50 µm.

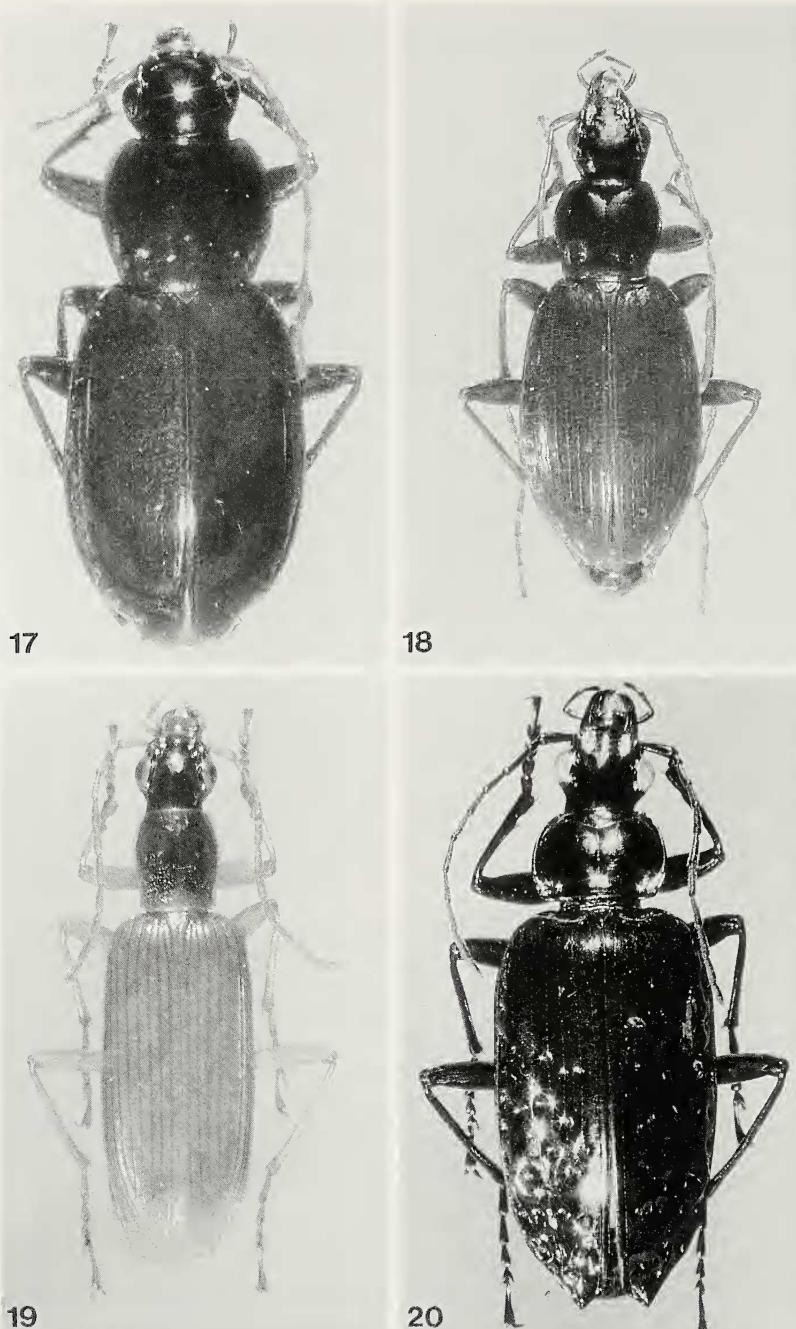


Fig. 17-20.—Photographs of habitus of representative species of *Onypterygia* species. Fig. 17, *O. pacifica*, n. sp. Holotype, male, TL = 6.7 mm. MEXICO, Oaxaca, 3.2 km. N San Jose del Pacifico (TAMU). Fig. 18, *O. stenapteryx*, n. sp. Holotype male, TL = 6.7 mm. MEXICO, Michoacan, 30.2 km. W. Uruapan (USNM). Fig. 19, *O. perissostigma*, n. sp. Paratype, male, TL = 7.4 mm. Mexico, Oaxaca, 27.2 km. S. Valle Nacional (USNM). Fig. 20, *O. polytreta*, n. sp. Paratype male, TL = 13.1 mm. PANAMA, Chiriqui, Pr. Cerro Pando (USNM).

Table 3.—Checklist of the species groups and species of *Onypterygia* Dejean.

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<i>O. famini</i> species group	<i>O. angustata</i> species group
<i>O. famini</i> Solier	<i>O. longispinis</i> Bates
<i>O. cyanea</i> Chaudoir	<i>O. angustata</i> Chevrolat
<i>O. wappesi</i> species group	<i>O. pseudangustata</i> , new species
<i>O. wappesi</i> , new species	<i>O. stribungi</i> , new species
<i>O. amecameca</i> , new species	<i>O. fulgens</i> species group
<i>O. atoyac</i> , new species	<i>O. iris</i> Chaudoir
<i>O. shpeleyi</i> , new species	<i>O. championi</i> Bates
<i>O. pacifica</i> , new species	<i>O. donato</i> Ball and Shpeley
<i>O. aeneipennis</i> species group	<i>O. chrysura</i> Bates
<i>O. batesi</i> , new species	<i>O. kathleenae</i> , new species
<i>O. aeneipennis</i> Chaudoir	<i>O. exeuross</i> , new species
<i>O. cupricauda</i> Casey	<i>O. polytreta</i> , new species
<i>O. stenapteryx</i> , new species	<i>O. crabilli</i> , new species
<i>O. pallidipes</i> Chaudoir	<i>O. quadrispinosa</i> Bates
<i>O. rubida</i> Bates	<i>O. scintillans</i> , new species
<i>O. perissostigma</i> species group	<i>O. fulgens</i> Dejean
<i>O. perissostigma</i> , new species	<i>O. tricolor</i> Dejean
<i>O. pusilla</i> species group	<i>O. hoepfneri</i> Dejean
<i>O. pusilla</i> Chaudoir	<i>O. sallei</i> Chaudoir
<i>O. rawlinsi</i> , new species	

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in the platynine group, with the implication that its truncatipennian (lebiomorph) features are convergent with that group, and do not comprise evidence of relationships.

What is *Onypterygia*? Although it is clearly a platynine, its position in the Platynini is not certain. This question remains as open now as when Whitehead (1973) surveyed the Mexican species of *Platynus*. The genus comprises the only beetles of the worldwide subtribe Platynina (sensu Habu, 1978) having pectinate tarsal claws, and its distribution is confined to the northern Neotropics. *Onypterygia* is distinguished from *Platynus* (Whitehead, 1973, and Liebherr, 1992) only by pectinate tarsal claws of adults. However, the pectinations are distinctive (long and curved mesoventrally), providing the basis to postulate that the genus is monophyletic.

Liebherr (1986:26) suggested that *Onypterygia* is derived from *Platynus*, and we do not disagree. However, we retain it as a genus because there is no formal reason to do otherwise. The approach is conservative: the genus has been considered valid since first proposed, and being still unbroken it requires no fixing.

#### Classification of Species

The 34 species of *Onypterygia* are arranged in seven species groups (Table 3). The Appendix (p. 408) provides an index to the names of the taxa, including junior synonyms.

#### Key to Adults of the Species of *Onypterygia* Dejean

1	Metathorax short, metepisternum with anterior and lateral margins about equal in length; metasternum between middle and hind coxae about half length of hind coxa . . . . .	2
1'	Metathorax longer (normally developed), metepisternum with lateral margin much longer than anterior margin; metasternum between middle and hind coxae equal or subequal in length to hind coxa . . . . .	7
2 (1)	Elytra bright metallic, striped alternately with metallic green and cupreous vittae;	

umbilical punctures foveate. Geographical range—Costa Rica . . . . .	
2' Elytra concolorous, slightly metallic or nonmetallic . . . . .	O. donato Ball and Shpeley, p. 356
3 (2') Pronotum with posterior pair of setigerous punctures distinctly anterad posterolateral angles (Fig. 30B). Color of body and elytra rufotestaceous. Interval 3 of elytron with only two setigerous punctures . . . . .	O. shpeleyi, n. sp., p. 319
3' Pronotum with posterior pair of setigerous punctures at or only slightly anterad posterolateral angles. Color of body and elytra rufotestaceous or darker . . . . .	4
4 (3') Elytron with apex of suture (interval 1) angulate or denticulate . . . . .	5
4' Sutural apex of elytron rounded, not angulate or denticulate . . . . .	6
5 (4) Elytra with interneurs deep; interval 3 tri- or bisetose. Geographical range—Mexico: Sierra Madre del Sur, Guerrero . . . . .	O. wappesi, n. sp., p. 315
5' Elytra with interneurs evanescent; interval 3 bisetose. Geographical range—Mexico: Sierra Madre del Sur, Oaxaca . . . . .	O. pacifica, n. sp., p. 320
6 (4') Body and leg color darker, piceous, elytra dull blue-green. Geographical range—Mexico: Transvolcanic Sierra, State of México . . . . .	O. amecameca, n. sp., p. 317
6' Color of body, legs, and elytra paler, rufotestaceous. Geographical range—Mexico: Sierra Madre del Sur, Guerrero . . . . .	O. atoyac, n. sp., p. 318
7 (1') Elytron with interneurs more deeply (normal) engraved, interneur 1 on apical declivity not deeper than interval 2; preapical lateral callus absent; sutural apex not angulate or denticulate . . . . .	8
7' Elytral interneur 1 near apex much deeper than interneur 2, or all interneurs shallowly engraved; preapical lateral callus distinct, indistinct, or absent; sutural apex angulate, denticulate, or rounded . . . . .	19
8 (7) Elytron with apex sharply angulate or acuminate (cf. Fig. 10); color distinctly metallic or not . . . . .	9
8' Elytron with apex rounded (cf. Fig. 7); color distinctly metallic . . . . .	10
9 (8) Color of elytral disc bright metallic green, with cupreous overtones posteriorly. Pronotum (Fig. 49B) with lateral margins markedly sinuate posteriorly, and posterolateral angles more pointed. Internal sac of male genitalia without spinose sclerites. Geographical range—Mexico: Sierra Transvolcanica, Nayarit . . . . .	O. rawlinsi, n. sp., p. 341
9' Color of elytral disc either bronze or dull bronze-green. Pronotum (Fig. 49A) with lateral margins less sinuate posteriorly, posterolateral angles more rounded. Internal sac of male genitalia (Fig. 50B) with single (basal) spinose sclerite . . . . .	O. pusilla Bates, p. 339
10 (8') Hind femur with dorsoapical setae (one or more) . . . . .	11
10' Hind femur without dorsoapical setae . . . . .	12
11 (10) Elytra metallic, green in most specimens, with cupreous reflections apically. Pronotum with two pairs of lateral setigerous punctures . . . . .	O. famini Solier (in part), p. 309
11' Elytra metallic, blue in most specimens, without cupreous reflections apically. Pronotum with single pair (posterior) of lateral setigerous punctures . . . . .	O. cyanea Chaudoir, p. 312
12 (10') Head with pronounced frontal carina on each side. Pronotum slender, as long as or longer than wide (Fig. 19, 47) and posterolateral impressions coarsely punctate; prosternum with apex of intercoxal process truncate. Sternum VII of female with row of five or six pairs of setigerous punctures near posterior margin . . . . .	O. perissostigma, n. sp., p. 335
12' Head without distinct frontal carinae laterally. Pronotum broader, with posterolateral impressions impunctate or finely punctate; prosternum with intercoxal process rounded apically. Female sternum VII with two pairs of marginal setigerous punctures . . . . .	13
13 (12') Pronotum in color entirely pale, or dark but with explanate lateral margins pale. Femora pale. Elytra metallic green or blue, without cupreous reflections apically. Geographical range—Mexico: Transvolcanic Sierra, Pacific drainages . . . . .	14
13' Pronotum dark, including beaded or explanate lateral margins. Femora pale or dark. Elytra metallic green, with evident to pronounced cupreous reflections apically. Geographical range—Mexico to El Salvador . . . . .	15
14 (13) Pronotum (Fig. 38) with lateral margins markedly sinuate posteriorly; posterolateral angles sharp. Geographical range—Mexico: Morelos and Puebla . . . . .	O. pallidipes Chaudoir, p. 330
14' Pronotum (Fig. 39) with lateral margins slightly sinuate posteriorly; posterolateral angles obtuse. Geographical range—Mexico: Michoacán and Colima . . . . .	O. rubida Bates, p. 332
15 (13') Pronotum (Fig. 21) with lateral margins not beaded, evenly curved, not sinuate poste-	

riorly; lateral grooves broad throughout their length. Geographical range—northeastern Mexico to El Salvador ..... *O. famini* Solier (in part), p. 309  
 15' Pronotum (Fig. 34–37) with lateral margins distinctly beaded or not; distinctly sinuate posteriorly; lateral grooves narrow throughout or widened basally only. Geographical range—Mexico: Sierra Madre Oriental, Transvolcanic Sierra, or Sierra Madre del Sur ..... 16

16 (15') Pronotum (Fig. 34) with lateral margins explanate, slightly sinuate posteriorly; postero-lateral angles obtuse; anterior lateral seta inserted ca. 1.5–3.0 diameter of setal puncture from margin. Geographical range—Mexico: Atlantic drainages of Sierra Madre Oriental, Transvolcanic Sierra, and Sierra Madre del Sur ..... *O. batesi*, n. sp., p. 325  
 16' Pronotum (Fig. 35–37) with lateral margins explanate to narrow, distinctly to markedly sinuate posteriorly; postero-lateral angles sharp; anterior lateral seta inserted ca. 1.0–1.5 diameter of setal puncture from lateral margin. Geographical range—Mexico: Pacific drainages of Transvolcanic Sierra and Sierra Madre del Sur ..... 17

17 (16') Appendages paler, femora rufous to rufopiceous. Geographical range—Mexico: state of México, and Michoacán ..... *O. stenapteryx*, n. sp., p. 329  
 17' Appendages darker, femora piceous to black. Geographical range—Mexico: Sierra Madre del Sur ..... 18

18 (17') Pronotum (Fig. 35) narrower, values for LP/WP more than 0.95. Geographical range—Mexico: Oaxaca ..... *O. aeneipennis* Chaudoir, p. 327  
 18' Pronotum (Fig. 36) broader, values for LP/WP less than 0.95. Geographical range—Mexico: Guerrero ..... *O. cupricauda* Casey, p. 328

19 (7') Pronotum (cf. Fig. 53) with lateral margins distinctly sinuate posteriorly; lateral setigerous punctures one or two pairs; postero-lateral angles sharp. Sternum VII of male with single pair of posterior marginal setigerous punctures, females with two pairs ..... 20  
 19' Pronotum (cf. Fig. 73) with lateral margins not distinctly sinuate; lateral setigerous punctures one or two pairs, or absent; postero-lateral angles various, from nearly rectangular to distinctly rounded ..... 23

20 (19) Pronotum with one pair (posterior) of lateral setigerous punctures ..... 21  
 20' Pronotum with two pairs of lateral setigerous punctures ..... 22

21 (20) Elytra green; apices obtusely angulate. Geographical range—Mexico: eastern Veracruz ..... *O. pseudangustata*, n. sp., p. 347  
 21' Elytra coppery or coppery green; apices acuminate (Fig. 10). Geographical range—Mexico: eastern Oaxaca ..... *O. striblingi*, n. sp., p. 348

22 (20') Elytron with apex acuminate (Fig. 10). Geographical range—Guatemala and Mexico: Chiapas ..... *O. longispinis* Bates, p. 344  
 22' Elytron with apex obtusely angulate. Geographical range—Mexico: Veracruz to Panama ..... *O. angustata* Chevrolat, p. 345

23 (19') Pronotum with two pairs of lateral setigerous punctures ..... 24  
 23' Pronotum with one pair (posterior) of lateral setigerous punctures, anterior pair absent ..... 27

24 (23) Elytra with alternating metallic green and cupreous vittae. Female with stylomere 2 of ovipositor slender, with few ensiform setae, and without lateral pad of setae (Fig. 12) ..... 25  
 24' Elytra metallic green, without alternate metallic green and coppery vittae. Stylomere 2 (Fig. 16A) stout, with lateral pad of ensiform setae ..... 26

25 (24) Elytron with apex broadly rounded, apex of interval 1 not angulate or denticulate. Sternum VII of female with more than two pairs of posterior marginal setae. Geographical range—Mexico: Veracruz ..... *O. iris* Chaudoir, p. 353  
 25' Elytron with apex acuminate (Fig. 10), apex of interval 1 subangulate to denticulate. Geographical range—Panama and Costa Rica ..... *O. championi* Bates, p. 354

26 (24') Elytron with apex obtusely angulate (Fig. 4B). Pronotum with lateral margins broad, not beaded; postero-lateral angles obtuse, but evident. Elytron with interval 3 trisetose. Abdominal sternum VII of female with two pairs of posterior marginal setae. Geographical range—Mexico: Chiapas, to Costa Rica ..... *O. chrysura* Bates, p. 356  
 26' Elytron with apex acuminate (Fig. 11A). Pronotum with lateral margins narrow, beaded; postero-lateral angles broadly rounded. Elytron with interval 3 bisetose, anterior setigerous puncture absent. Sternum VII of female with more than two pairs of posterior marginal setae ..... *O. kathleenae*, n. sp., p. 358

27 (23') Pronotum (Fig. 54A, B) with postero-lateral angles angulate. Size smaller, TL less than 10.0 mm. Sternum VII of female with only two pairs of posterior marginal setae ..... 28

27'	Pronotum (Fig. 67-74) with posterolateral angles rounded. Size larger, TL greater than 11.0 mm. Abdominal sternum VII of female with more than two pairs of marginal setae	29
28 (27)	Elytra green; apices obtusely angulate. Geographical range—Mexico: eastern Veracruz	347
28'	Elytra coppery or coppery green; apices acuminate (Fig. 10). Geographical range—Mexico: eastern Oaxaca	348
29 (27')	Elytron with disc plurifoveate; umbilicate setigerous punctures moderately to markedly foveate. Geographical range—Costa Rica to Panama	30
29'	Elytron with disc not plurifoveate, setigerous punctures of interval 3 foveate or not; umbilicate setigerous punctures foveate or not. Geographical range—Mexico to Panama	31
30 (29)	Elytra without alternate metallic green and coppery vittae; interneurs obsolete, each marked only by large punctures; interneur 1 toward apex not impressed. Geographical range—Costa Rica	362
30'	Elytra with alternate metallic green and coppery vittae; interneurs each marked by row of fine, closely set punctures in addition to large foveae on intervals 3, 5, and 7 (Fig. 77); interneur 1 apically clearly impressed. Geographical range—Panama	361
31 (29')	Pronotum (Fig. 67) with lateral margins posteriorly narrow, beaded. Elytron with apex acuminate (Fig. 11A), extended markedly. Geographical range—southern Mexico	359
31'	Pronotum (Fig. 69) with lateral margins posteriorly wide, not beaded. Elytron with apex obtusely angulate to biacuminate	32
32 (31')	Elytron with umbilicate series of setigerous punctures markedly foveate.	33
32'	Elytron with umbilicate series not markedly foveate.	34
33 (32)	Elytron with apex and sutural apex acuminate. Geographical range—Guatemala	34
33'	Elytron with apex rounded, apex of interval 1 (sutural apex) only angulate or denticulate, not acuminate. Geographical range—Costa Rica	364
34 (32')	Pronotum without lateral setigerous punctures. Elytra metallic green or blue, with or without coppery reflections. Geographical range—northern Mexico to northern South America	366
34'	Pronotum with single pair (posterior) of lateral setigerous punctures. Elytra of various colors	35
35 (34')	Elytra bicolored, basal half rufotestaceous, apical half dark violaceous; apex of elytron sharply denticulate. Geographical range—northern Mexico to northern South America	370
35'	Elytra concolorous; apex of elytron sharply bidenticulate or not	36
36 (35')	Elytra shiny, each with conspicuous preapical callus, laterally. Pronotum with posterolateral impressions markedly punctate. Geographical range—Mexico: central Veracruz	377
36'	Elytra less shiny, with preapical calli inconspicuous. Pronotum with posterolateral impressions not markedly punctate. Geographical range—central Mexico (excluding Veracruz) to Honduras	375

### The *famini* Species Group

#### Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small to moderate in size (TL 9–11 mm), with head dorsally and pronotum dark metallic green, elytra with disc concolorous metallic green or blue, with or without cupreous reflections laterally. Pronotal lateral setae one or two pairs, each elytron with three discal setae in or adjacent to interval 3, hind femur with or without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with two pairs. Pronotum (Fig. 21, 22) with lateral margins curved evenly, or slightly sinuate posteriorly, not beaded, lateral grooves wide; posterior

pair of lateral setigerous punctures near posterolateral angles, slightly removed from margins. Elytral apices are broadly rounded (Fig. 7), sutural apices rounded, not denticulate (cf. Fig. 8), and dorsal surface without preapical lateral calli (cf. Fig. 11B:pc).

### Description

With diagnostic combination of the *famini* species group and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

**Color.**—Ventral surface of body and appendages (except apical antennomeres and elytra) black to piceous.

**Microsculpture.**—Head with mesh pattern clearly evident to indistinct, isodiametric, but on clypeus slightly transverse. Pronotum with mesh pattern transverse, microlines fine but evident throughout. Elytra with mesh pattern isodiametric, lines fine but evident throughout.

**Luster.**—Dorsal surface moderately shining.

**Head.**—Frons and vertex smooth, without supraorbital carina each side. Eyes of average convexity.

**Prothorax.**—Pronotum sparsely punctate posterolaterally; posterior pair of setigerous punctures near posterolateral angles. Anterior bead complete or incomplete; lateral beads absent medially and anteriorly; posterolateral impressions impunctate or sparsely punctate; posterolateral angles broadly rounded. Prosternum with intercoxal process rounded apically.

**Pterothorax.**—Mesepisternum generally punctate. Metathorax fully developed, metepisterna distinctly longer than wide.

**Elytra.**—Surface smooth. Elytron with humerus broadly rounded, developed normally; lateral margin slightly rounded; apex rounded; sutural apex rounded; discal and umbilical punctures not foveate. Interneurs 1 and 2 posteriorly on apical declivity about equally deeply impressed; interneurs 2–6 punctate for most of length.

**Hind Wings.**—Macropterous; wedge cell (Fig. 23:w) elongate, with short sides equal to one another.

**Legs.**—Tarsomeres 1–3 of middle and hind tarsi sulcate laterally. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe shorter than basal portion. Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11F:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

**Male Genitalia.**—Median lobe with apical portion short (Fig. 24A:ap), internal sac relatively short, with two or three patches of long setiform spines (Fig. 25C:s:sp), without basal or preapical lobes.

**Ovipositor.**—Stylomere 2 (Fig. 26) form 1, dorsolateral margin with about ten ensiform setae.

### Habitat

Adults of this species group have been collected in tropical deciduous, tropical montane, oak, and oak-pine forests, from near sea level to 2300 m altitude.

### Geographical Distribution

The range of this species group extends from northwestern Mexico southward to El Salvador (Fig. 27).

### Chorological Affinities

Species of the *O. famini* species group are known to occur with those of the *aeneipennis*, *angustata*, *pusilla*, and *fulgens* species groups, and to overlap the ranges of the *wappesi* and *perissostigma* groups.

### Included Species

Two species are included in this group: *O. famini* Solier and *O. cyanea* Chaudoir.

#### *Onypterygia famini* Solier (Fig. 2, 6A–F, 7, 21, 23, 24, 26, 27)

*Onypterygia famini* Solier (1835:113). Type material: not found (expected to be in MNHP, and sought there unsuccessfully by Whitehead in 1968, and by Ball in 1972). Bates, 1882:131.

*Onychopterygia famini*; Gemminger and Harold, 1868:384. Chaudoir, 1878:276.

*Onypterygia viridipennis* Chevrolat, 1835:158. Lectotype (here designated): slightly teneral male in excellent condition, labelled "Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909 E. B. Poulton." and

"TYPE COL: 148 2/2 *Onypterygia viridipennis* Chevr. HOPE DEPT. OXFORD" (OXUM). Chaudoir, 1878:276.

*Onypterygia humilis* Chevrolat, 1835:159. Lectotype (here designated): male labelled "humilis Chv. famini Sol. fulgidipennis Lap." and "Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909, E. B. Poulton." (OXUM). Chaudoir, 1878:276.

*Onypterygia fulgidipennis* Castelnau, 1840:42. Type material: not found (expected to be in MNHP, and sought there unsuccessfully by Whitehead in 1968, and by Ball in 1972). Chaudoir, 1878: 276.

#### Type Material

We have not seen type material of *O. famini* or of *O. fulgidipennis*, but we accept the synonymy proposed by Chaudoir (1878:276). Specimens of *O. humilis* and *O. viridipennis* in Chevrolat material at the Hope Museum are fully typical of *O. famini*, and lectotypes were selected as indicated. The specimen of *O. humilis* was displaced in the collection, but according to Ernest Taylor (personal communication) it is the only specimen available as a possible type. A female specimen of *O. viridipennis* labelled "TYPE COL: 148 1/2. . ." in the Hope Museum is a composite of an *O. famini* hind body with the fore body of some other species.

#### Type Localities

The type area is Mexico for *O. famini*, *O. humilis*, and *O. fulgidipennis*. Here, we restrict the type locality to 10 km northwest of Jalapa. The type locality of *O. viridipennis* is Las Vigas, Veracruz, Mexico.

#### Diagnostic Combination

Adults of this species have the features of the *O. famini* species group, elytra metallic green with cupreous reflections laterally, and the pronotum with two pairs of marginal setae.

#### Description

With diagnostic combination of *O. famini* and the following.

*Measurements and Proportions*.—Size small to intermediate (TL 9.0–11.5 mm), WP/WH intermediate (1.31), LP/WP intermediate (0.90), WP/WPb low (1.20), LE/WE intermediate (1.64).

*Color*.—Apical antennomeres rufopiceous. Elytra bright green, laterally with cupreous reflections.

*Microsculpture*.—Elytra, as in Figure 2.

*Chaetotaxy*.—Pronotum, lateral setae two pairs.

*Mouthparts*.—Mandibles as in Figure 6A–F.

*Prothorax*.—Pronotum (Fig. 21). Anterior bead complete, or incomplete; posterolateral impressions sparsely punctate; angles broadly rounded; lateral margins sinuate.

*Hind Wings*.—Macropterous. Venation as in Figure 23.

*Male Genitalia*.—As in Figure 24A, B.

*Ovipositor*.—Stylomeres 1 and 2 as in Figure 26.

#### Variation

Pronotal form is quite varied, in some specimens much like that shown for *O. cyanea* (Fig. 22), except for having both pairs of marginal setae. Pronotal sides tend to be more markedly sinuate and the posterolateral angles more prominent in specimens from Hidalgo, San Luis Potosi, and Veracruz than in specimens from Chiapas, but extremes are present in both areas. One specimen from near Chiapa de Corzo is notably small, relatively dull (metallic luster slight), and has convex elytral intervals and relatively coarse microsculpture. The elytra of a specimen from Los Amates appear blue from above but are clearly green and faintly cupreous from behind.

### Habitat

Specimens of *O. famini* have been taken in moderately dry to moderately wet forests, chiefly oak, at middle altitudes (732–2286 m) in Mexico. Specimens have been taken in bromeliads (December, January, February, April, and May), others at UV lights (May and June), and some in moss on rocks (November). These records suggest active flight during the summer wet season and adult quiescence in the winter dry season.

In Guatemala, several specimens of this species were collected at night, at UV light traps, in tropical montane forest. In spite of intensive efforts to find them, no specimens were collected in the vicinity of the light traps during daylight hours, and so perhaps the nocturnally active individuals had flown into the area from elsewhere.

### Geographical Distribution

The range of *O. famini* extends from San Luis Potosí in northeastern Mexico and the Sierra Madre del Sur in Oaxaca south at least to El Salvador, and perhaps Costa Rica (Fig. 27). We have not verified Middle American records listed by Bates (1882:131), but we found specimens from all Mexican localities except Las Vigas, Veracruz, in BMNH and MNHP. The record from Puebla may refer to a locality other than the city of that name.

### Chorological Affinities

The range of *O. famini* is allopatric in relation to the range of its close relative, *O. cyanea* (Fig. 27).

### Phylogenetic Relationships

This species is postulated to be the adelphotaxon of *O. cyanea* Chaudoir. Although the two species seem to be closely related on the basis of many shared features, and although they are parapatric or marginally sympatric, we have not seen evidence of intergradation.

### Material Examined

About 130 specimens of *O. famini* were seen, from the following localities. **MEXICO. Chiapas:** 11.5 km S Amatenango del Valle, Jct. Hwy. 190 & 195, nr. Chiapa de Corzo, 1 male, 2 km S Chicoasén, on rd. to Mirador, VI.18.1989, H. F. Howden (UASM); 1 female, El Chorradero, 8 km E Chiapa de Corzo, VI.6.1989, H. F. Howden (UASM); 1 male, El Aguacero Parque, VI.22.1990, J. Huether (JEWC); 3 males, 3 females, 4.8 & 12.4 km S Frontera Comalapa, 743 m, U-V light, VI.15–17.1966, Ball & Whitehead (UASM); 1 male, 47 km N. Huixtla, 1311 m, bromeliads, II.26.1966, Ball & Whitehead (UASM); Los Amates (UASM); 1 female, 1 km S Ocosingo, X.18.1988, H. & A. Howden (RHTC); 1 female, 5 km E Ocozocoautla, 820 m, VI.4.1990, H. & A. Howden (UASM); 1 male, 1 female, Parque Nacional Sumidero, 1000 m, V.25.1990, H. & A. Howden (UASM); 1 male, 3 females, 5 km S Pueblo Nuevo, 1646 m, in bromeliads, IV.27.1966 (UASM); 1 female, Rancho Nuevo, 14 km SE San Cristóbal de las Casas, VIII.30.1965, D. E. Breedlove (CASC); Ruinas Chinultic, 1500 m—3 males, VI.3.1990, H. & A. Howden (CMNC); 2 females, VI.12.1989, H. F. Howden (UASM); 1 male, 1 female, VI.12.1990 (UASM); 1 male, 3 females, Clark & Cave (AUEM); 1 male, X.18.1988, R. H. Turnbow (RHTC); San Cristóbal de las Casas (UASM); 27.4 km SE Teopisca (UASM). **Hidalgo:** 1 female, Atexca, V.26.1979, M. Zunino (ACCS); NE Jacala—1 female, 38 km, 1372 m, V.27.1974 (UASM); 2 males, 1 female, V.27.1974, O'Brien, O'Brien & Marshall (UASM); 3 males, 2 females, 46.7 km, V.27.1974, O'Brien, O'Brien & Marshall (UASM). **Oaxaca:** 30 km S Sola de Vega (UASM). **Puebla:** Puebla. 1 male, Xicotepetec de Juárez, 1200 m, at mercury light (CASC). **San Luis Potosí:** 1 female, 30 km E Landa de Matamoros, 1524 m, XI.18–19, 1965, Ball & Whitehead (UASM); 1 male, Xilitla, VI.17.1963, D. R. Whitehead (UASM). **Veracruz:** Cerro de Palmas, Jalapa, 5 and 10 km NW Jalapa; 35 km E Jilotepec, Las Vigas (Bates, 1882); Orizaba; 1 female, Orizaba, Mann & Skewers (MCZC); 1 male, Río Juwapa, XI.6.1975, D. Figueroa (UNAM). **COSTA RICA.** Costa Rica (Bates, 1882). **EL SALVADOR. La Libertad:** Boquerón. **GUATEMALA. Alta Verapaz:** Senahú (Bates, 1882). **Baja Verapaz:** 1 male, 9.6 km W Chilascó, 1560 m,

humid oak-pine forest, U-V light, 91-21, V.25.1991 (UASM); Purulhá (Bates, 1882); 8 km S Purulhá, 1660 m, tropical montane forest, U-V light, Ball, Ball & Shpeley (UASM)—1 male, 1 female, V.19.1991; 2 males, 1 female, V.20.1991; 1 female, VI.1.1991. **Huehuetenango:** 55 km NW Huehuetenango, Río Selegua. **Sacatepequez:** Capetillo (Bates, 1882).

### *Onypterygia cyanea* Chaudoir

(Fig. 22, 25A-D, 27)

*Onychopterygia cyanea* Chaudoir, 1878:277. Lectotype (here selected): male, labelled "Ex Musaeo Chaudoir" (Chaudoir-Oberthür box 293/2/5, MNHP).

*Onypterygia cyanea*; Bates, 1882:132.

*Onypterygia valdestriata* Bates, 1884:286. Type specimen: male, labelled "TYPE H. T." [circular, ringed with red], B.C.A. COL. I.I. *Onypterygia valdestriata*, Bates", "Pinos Altos, Chihuahua, Mexico. Buchan-Hepburn" (Drawer 361/4/5, BMNH). New synonymy.

#### Type Material

*Onypterygia cyanea* was described explicitly from Oaxaca, based on four specimens of Sallé material. We found no specimens so labelled in Chaudoir material (MNHP), but did find one male and two females without locality data; the male is selected here as lectotype.

#### Type Localities

For *O. cyanea*, the type locality is Oaxaca, Mexico. For *O. valdestriata*, it is Pinos Altos, Chihuahua. Bates cited the type locality of *O. valdestriata* as "Chihuahua" only, but labelling on the holotype is more specific.

#### Diagnostic Combination

With character states of the *O. famini* species group, restricted as follows. With noncupreous, blue (few specimens green or purple) elytra and only one (postero-lateral) pair of marginal setae on pronotum; apical antennomeres rufous (slightly paler than those of *O. famini*).

#### Description

With diagnostic combination of *O. cyanea* and the following.

*Measurements and Proportions*.—TL intermediate (9.5–10.5 mm); (proportions for male from 8.7 km E Cuernavaca, Morelos), WP/WH intermediate (1.38), LP/WP intermediate (0.90), WP/WPb low (1.19), LE/WE intermediate (1.65). Same of male from Sierra Charuco, Río Mayo, Sonora: WP/WH 1.34, LP/WP 0.92, WP/WPb 1.17, LE/WE 1.53.

*Prothorax*.—Pronotum (Fig. 22); posterolateral impressions impunctate, or sparsely punctate.

*Male Genitalia*.—As in Figure 25A-D.

#### Variation

Elytra are notably greenish in a specimen from Atzimba, notably purplish in one from Pinos Altos. Pronotal form varies much as in *O. famini*; most specimens from Morelos have markedly sinuate lateral margins and distinct posterolateral angles, and so resemble more closely specimens of *O. famini* from Veracruz than from Chiapas. Specimens from Sonora and Chihuahua differ from all others by much more distinct punctuation on elytral interneurs, sides of metasterna, mesepisterna, and proepisterna; they may differ also by smaller patches of spines on the internal sac and by some body proportions.

#### Habitat

This species lives in more arid regions than does *O. famini*. Most records are from early June to early August, but one is from September (Cuernavaca). There are no dry season records, nor records from bromeliads. The longest series (eight specimens) was collected at UV light, in tropical deciduous forest, 8.7 km east of Cuernavaca, Morelos, June 29–30, 1966.

### *Geographical Distribution*

The range of this species extends from western Mexico (Sonora and Chihuahua) south to Oaxaca (Fig. 27).

### *Chorological Affinities and Phylogenetic Relationships*

See these topics for *O. famini*, above.

### *Material Examined*

Approximately 120 specimens of *O. cyanea* were seen, from the following localities. Specimens from all localities listed by Bates (1882:132) are in BMNH or MNHP.

**MEXICO.** **Chihuahua:** 6 males, 6 females, 6.4 km N. Las Chinacas, 1271 m, U-V light, VII.9-10.1989, S. McCleve (UASM); Pinos Altos (Bates, 1882); 1 female, 9.7 km S Yécora (Sonora), 1752 m, U-V light, VII.2-3.1990, S. McCleve (UASM). **Colima:** 14.5 km N Comala; 2 males, 2 females, El Terrero, X.4.1992, R. H. Turnbow (RHTC); 3 females, W. rd. to El Terrero, 914.4-1524 m, X.3-5.1992, J. E. Wappes (JEWC); 1 male, 3 females, 38.4 km W Villa Alvarez, X.5.1992, R. H. Turnbow (RHTC). **Durango:** 1 male, 3.2 km N. Pueblo Nuevo, R. H. Scheibner (MSUC). **Guerrero:** 1 female, Acahuizotla, VI.22.1982, M. Garcia (CASC); 4 km NE Cacahuamilpa (TAMU). Chilpancingo (USNM); 29 km S Chilpancingo; 15.4 km SW jct. Hwy 195 & rd. to Filo de Caballo (UASM); Taxco (CASC); Rte. 134, 67.1 km NE jct. w/Hwy 200 (UASM); 1 male, 8 km S Mazatlán, Hwy. 95, 830 m, VI.29.1992, C. L. Bellamy (CMNH). **Jalisco:** Ajijic (UASM); 1 male, 20 km N. Autlán, IX.28.1991, J. E. Wappes (JEWC); 32 km SW Autlán (CDAE). 11.7 km S Cocula (UASM); 1 female, Microondas San Francisco (Autlán), X.6.1992, R. H. Turnbow (RHTC); 1 female, 10 km W Chapala, VI.30.1963 (CISC); 1 male, Guadalajara (CMNH); 2 males, 1 female, 33.8 km S Puerto Vallarta, Hwy. 200, 725 m, U-V light, S. McCleve, P. Jump (UASM); 1 female, Puerto Vallarta, VI.19.1961, P. R. Grant (CNCI). **México:** 5 & 7 km NE Ixtapan (TAMU); Temascaltepec (CASC). **Michoacán:** 1 male, 19 km S Tzitzio on Huetamo rd., 19°20'N., 100°50'W., VII.10.1947, T. H. Hubbell (UMMZ). **Morelos:** Alpuyeca (USNM); Cuernavaca (USNM); 1 male, Cuautla, VI.20.1971, H. Brailovsky (CUCI); 1 male, 1 female, 19 km E Cuernavaca, Cañon de Lobos, 1120-1375 m, VII.3.1992, C. L. Bellamy (CMNH). **Nayarit:** 1 female, 21 km W Chapalilla, X.9.1992, R. H. Turnbow (RHTC); 9.7 km N. Compostela. 1 female, El Pichón, VI.29.1963, J. Doyen (CISC); La Mesa de Nayar (CASC); Tepic (CDAE); 2 males, 7 females, 23 km S Tepic, 1067 m, VII.17.1977, J. E. Rawlins (CMNH); 37 km SE Tepic; 1 male, 2 females, Volcán Ceboruco, 4-11 km W Jala, X.8-9.1992, R. H. Turnbow (RHTC). **Oaxaca:** Ixtapa; 1 male, Km 30, Carretero Miahualtán-Puerto Angel, 2200 m, X.21.1982, H. Brailovsky (CASC); 2 males, 1 female, Mun. Juquila, San Juan Lachao, IV.14.1965, G. Halfter (CNCI). **Sinaloa:** 1 female, 6-7 km N. La Capilla del Taxte, X.5.1990, R. H. Turnbow (RHTC); 2 males, 7 km NE La Capilla del Taxte, VI.27.1977, J. E. Rawlins (CMNH); 1 male, 13 km W El Palmito, VII.1964, H. F. Howden (CNCI). **Sonora:** 2 males, 1 female, 5.1 km NW Huibache, 1577 m, U-V light, VII.11-13.1989, S. McCleve (UASM); Sierra Charuco, Río Mayo; 1 male, 6.1 km S Santa Rosa, 1000 m, U-V light, Sinaloan thorn scrub, VII.09.1993, S. McCleve, G. E. & K. E. Ball (UASM); 1 male, 23.2 km NW Yécora, 1680 m, U-V light VII.08.1993, S. McCleve, G. E. & K. E. Ball (UASM); 1 male, 6.4 km NE Yécora, 1547 m, VI.30-VII.1.1990, S. McCleve (UASM).

### The *wappesi* Species Group

#### *Diagnostic Combination*

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small in size (TL ca. 5-8 mm), head dorsally and pronotum rufous to black, elytra dull metallic green or blue, without cupreous reflections, or piceous or rufous. Pronotal lateral setae one or two pairs, each elytron with two or three discal setae in or adjacent to interval 3, hind femur without dorsoapical setae, abdominal sterna IV-VI each with one pair of ambulatory setae, and abdominal sternum VII of males with one pair of posterior marginal setae, females with two pairs. Pronotum (Fig. 28-30B) with lateral grooves narrow, lateral margins posteriorly slightly sinuate or not, laterally and anteriorly beaded or not, and posterior pair of lateral setigerous punctures slightly or markedly anterad posterolateral angles, removed from lateral margins not on beads. Metathorax short, metepisternum quadrate, with anterior and lateral margins about equal to one

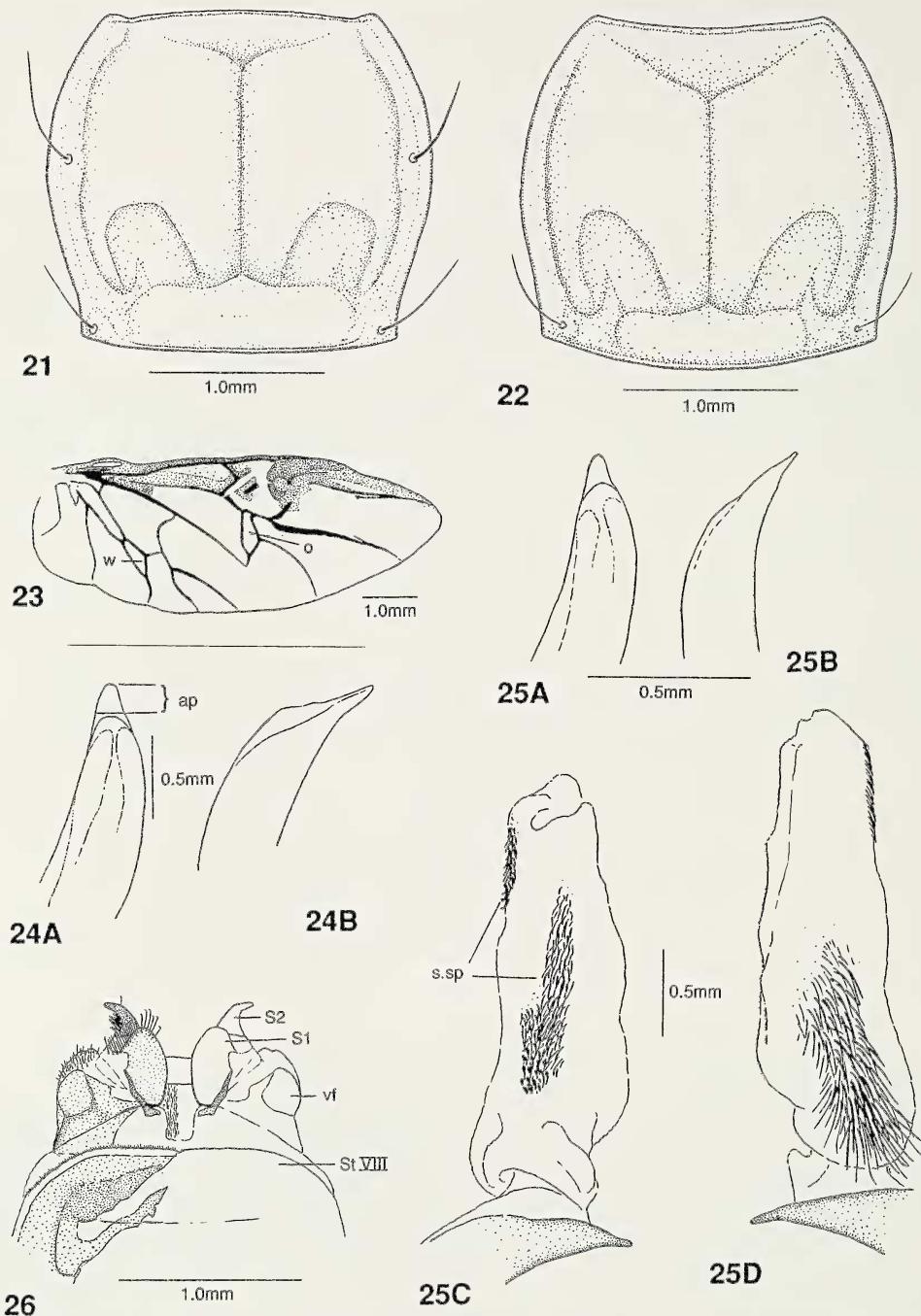


Fig. 21–26.—Line drawings of adult structural features of species of the *O. famini* group. Fig. 21, 22, pronotum, dorsal aspect: 21, *O. famini* Solier; 22, *O. cyanea* Chaudoir. Fig. 23, left hind wing of *O. famini* Solier. Fig. 24, 25, male genitalia: 24, *O. famini* Solier: A and B, median lobe, apical portion, dorsal and left lateral aspects, respectively; 25, *O. cyanea* Chaudoir: A, B, median lobe, dorsal and lateral aspects, respectively; C, D, internal sac, left and right lateral aspects, respectively, showing

another. Elytral apex rounded, sutural apex denticulate or rounded, interneurs about equally distinct, and preapical lateral calli absent.

#### Description

With diagnostic combination of *famini* group, and the following. Body rather small on average, measurements and proportions as in Table 2.

**Color.**—Body and appendages (except elytra) piceous to rufous only; elytra dull metallic green or blue, without cupreous reflections, to rufous (same color as body); other appendages of same color as body.

**Microsculpture.**—Head dorsally with microlines fine, nearly effaced, mesh pattern isodiametric. Pronotum with microlines very fine, nearly effaced, mesh pattern transverse. Elytra with microlines distinct, mesh pattern isodiametric or markedly transverse.

**Luster.**—Dorsal surface dull to moderately bright, elytra slightly iridescent or not.

**Head.**—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

**Prothorax.**—Pronotum (Fig. 28–30B), surface sparsely punctate posterolaterally; lateral margins beaded or not, slightly sinuate posteriorly or not; posterolateral angles various. Prosternum with intercoxal process rounded apically.

**Elytra.**—Humeri sloped, not rounded. Discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly on apical declivity about equally deeply impressed, or interneurs virtually absent, surface nearly smooth.

**Hind Wings.**—Brachypterous, short stubs.

**Legs.**—Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11F:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

**Male Genitalia.**—Median lobe with apical portion short, apex narrowly rounded (Fig. 31A, B). Internal sac variously armored: with single left median spinose sclerite (Fig. 32B, C), with basal and median ventral spinose sclerites (Fig. 31C), or without spinose sclerites (Fig. 32A).

**Ovipositor.**—Stylomere 2 form 1, as in Figure 12A, with about eight ensiform setae on or near dorsolateral margin.

#### Habitat

The species of the *wappesi* species group occupy tropical montane, riparian-alder, and dry pine-oak forests, from about 1700 to 2200 m altitude.

#### Geographical Distribution

This group is known only from Mexico, on the lower western slopes of the Sierra Madre del Sur, and from the Transvolcanic Sierra (Fig. 33).

#### Chorological Affinities

See "Chorological Affinities" for *famini* species group, above.

#### Included Species

Five species are included, all undescribed: *O. wappesi*, *O. amecameca*, *O. atoyac*, *O. shpeleyi*, and *O. pacifica*.

#### *Onypterygia wappesi*, new species (Fig. 8, 12, 28, 31A–C, 33)

#### Type Material

Eleven specimens. Holotype male, labelled: "MEX., Guerro./Hwy 134, 67 km NE/jet 200, VII.14.85/J. E. Wappes" (USNM). Allotype female, labelled same as

←  
spine fields. Fig. 26, sternum VIII and ovipositor sclerites of *O. famini* Solier. Legend: ap—median lobe, apical portion; o—oblongum cell; S1, S2—stylomeres 1 and 2, respectively; S.sp.—setiform spine; St VIII—sternum VIII; Vf—valvifer; w—wedge cell.

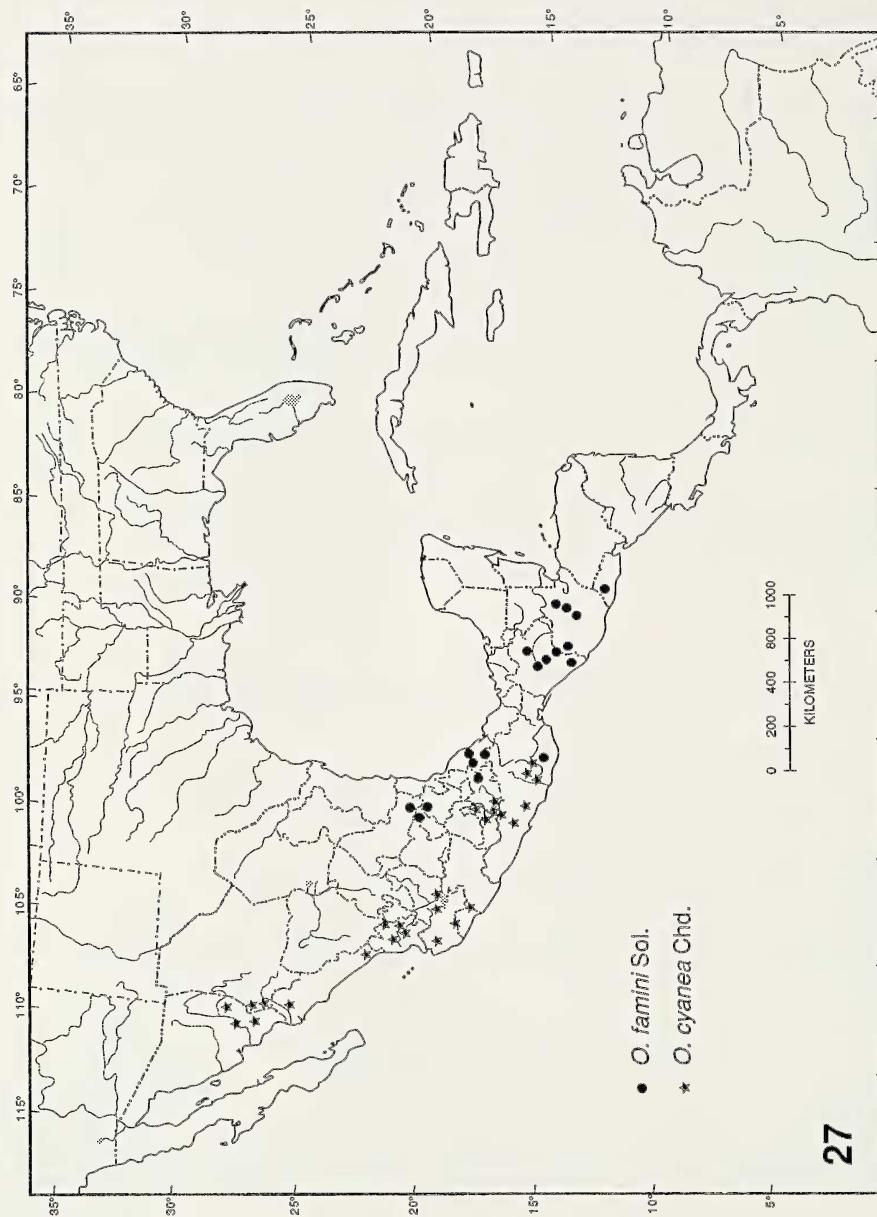


Fig. 27.—Map of southern North America, Middle, and northern South America, showing approximate positions of collecting records for species of the *O. famini* group.

holotype (USNM). Paratypes, nine females, one labelled same as holotype (JEW), eight labelled: "MEXICO Guerrero/hwy. 134 66.4 km NE jct./Hwy 200, 15 July 1985/R. Turnbow" (BMNH, CUIC, MNHP, RHTC, UASM).

#### *Specific Epithet*

Based on the surname of our friend, James E. Wappes, who, during his many trips to Middle America to collect cerambycids, has collected numerous carabids from interesting localities, and has made them available to us for study.

#### *Diagnostic Combination*

With character states of *O. wappesi* species group, and combination of rufopiceous color, small posterolateral pronotal impressions, elytral interneurs of average depth, angulate sutural apices, and trisetose interval 3.

#### *Description*

With diagnostic combination of *O. wappesi* and the following.

*Measurements and Proportions of Holotype*.—TL small (8.8 mm), WP/WH low (1.56), LP/WP low (0.86), WP/WPb high (1.40), LE/WE low (1.48).

*Color*.—Head piceous-black. Antennae with basal and apical antennomeres rufopiceous. Palpi piceous. Pronotum piceous-black. Elytra with discal pattern concolorous, dull green. Femora rufopiceous; tibiae and tarsi rufopiceous.

*Microsculpture*.—Mesh pattern of elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae three.

*Prothorax*.—Pronotum (Fig. 28). Anterior bead complete. Lateral margins not sinuate, beaded narrowly, posterolateral pair of setigerous punctures slightly in advance of posterolateral angles.

*Pterothorax*.—Mesepisternum generally punctate.

*Elytra*.—Elytron (Fig. 8) with lateral margin broadly rounded; sutural apex rounded. Interneurs 2–6 continuous, moderately deep, punctate for part of length.

*Legs*.—Tarsomeres 1–3 of midtarsi and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—(Fig. 31A–C) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; basal lobes absent; preapical lobes absent; armature one spinose sclerite.

*Ovipositor*.—Stylomeres 1 and 2 as in Figure 12.

#### *Geographical Distribution*

This species is known from the localities for the type series only (Fig. 33).

#### *Chorological Affinities*

Localities for this species, *O. shpeleyi*, and *O. atoyac* are in close proximity. Probably they are sympatric. Additionally, *O. cupricauda* (*aeneipennis* species group) probably is sympatric with *O. wappesi*, and the wide-ranging species of the *fulgens* species group probably occur in the same area, as well.

#### *Material Examined*

We saw the type series only; see above for details.

### *Onypterygia amecameca, new species* (Fig. 33)

#### *Type Material*

Holotype female, labelled: "Amecameca/ Mex./VII.8.1897"; "Koebele Collection" [dull orange paper]; "PN drawn/D. Hollingdale/1990" (CASC).

#### *Type Locality*

Amecameca, state of México, Mexico.

#### *Specific Epithet*

A noun in apposition, based on the name of the type locality.

### *Diagnostic Combination*

With character states of the *O. wappesi* species group, restricted as follows. Body and legs piceous, elytra rather dull metallic blue-green, pronotum with posterolateral angles obtusely angulate, posterolateral impressions broad, coextensive laterally with lateral grooves, elytra with interneurs shallow but sharp basally, less distinct on apical declivity, scutellar apices rounded, and interval 3 bisetose.

### *Description*

With diagnostic combination of *O. amecameca*, and the following.

*Measurements and Proportions of Holotype*.—TL small (5.20 mm), WP/WH low (1.41), LP/WP low (0.83), WP/WPB low (1.20), LE/WE low (1.42).

*Color*.—Head piceous-black. Antennae with basal and apical antennomeres rufostaceous, or taceous. Palpi piceous. Pronotum piceous-black. Elytra with discal pattern concolorous; blue-dull. Femora rufopiceous; tibiae and tarsi rufopiceous.

*Microsculpture, Mesh Pattern*.—Elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae two.

*Prothorax*.—Pronotum. Anterior bead complete. Lateral beads absent. Lateral margins sinuate, bead-ed posteriorly. Posterolateral pair of setigerous punctures at posterolateral angles.

*Pterothorax*.—Mesepisternum partially punctate.

*Elytra*.—Elytron, lateral margin broadly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow, impunctate.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe shorter than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

### *Geographical Distribution*

This species is known from the type locality only, which is located in a high-altitude internal drainage basin (Fig. 33).

### *Chorological Affinities*

*Onypterygia amecameca* is widely isolated from the other members of the *wappesi* species group. *Onypterygia fulgens* (*fulgens* species group) might be sympatric with *O. amecameca*.

### *Material Examined*

We have seen the holotype of *O. amecameca* only; see above for details.

### *Onypterygia atoyac, new species* (Fig. 30A, 32B, 33)

#### *Type Material*

Holotype female, labelled: “MEX. Guer. 73.8km/ne Atoyac de Alvarez/cloud for.: stream/arroyo; litter; 2340 m/August 12, 1983 83-75”; “MEXICO EXPED. 1983/H. E. Frania & R. J. Jaquumagi/Collectors”; “PN DRAWN/D. Hollingdale/1990” (USNM).

#### *Type Locality*

73.8 km northeast of Atoyac de Alvarez, Guerrero, Mexico.

#### *Specific Epithet*

A noun in apposition, based on the name of the mountain range within which the type locality is located.

### *Diagnostic Combination*

Character states of the *O. wappesi* species group, and integument generally rufous (specimen may be teneral), shining but not metallic, pronotum with posterolateral impressions narrow, lateral margins evenly constricted posteriorly, not sinuate, posterolateral angles obtuse, angulate, elytral interneurs shallow but distinct, punctate, elytral apices rounded, and interval 3 bisetose.

### Description

With diagnostic combination of *O. atoyac* and the following.

*Measurements and Proportions of Holotype*.—TL small (5.2 mm), WP/WH low (1.38), LP/WP low (0.78), WP/WPb intermediate (1.29), LE/WE low (1.47).

*Color*.—Head rufopiceous. Antennae with basal and apical antennomeres testaceous. Palpi rufous. Pronotum rufopiceous. Elytra with discal pattern concolorous, bronze; epipleura testaceous, same as ventral surface. Femora rufotestaceous; tibiae and tarsi rufotestaceous.

*Microsculpture, Mesh Pattern*.—Elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae two pairs. Elytron, discal setae two.

*Prothorax*.—Pronotum (Fig. 30A). Anterior bead complete. Lateral margins sinuate, not beaded. Posterolateral pair of setigerous punctures at posterolateral angles.

*Pterothorax*.—Mesepisternum partially punctate.

*Elytra*.—Elytron, lateral margin broadly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow; impunctate.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—(Fig. 32B) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; armature, one spinose sclerite on left side; microtrichial fields extensive, microtrichia short, pointed sharply.

### Geographical Distribution

Known from the type locality only, in the western part of the Sierra Madre del Sur (Fig. 33).

### Chorological Affinities

The known localities for this species, *O. wappesi* and *O. shpeleyi*, n. sp., are in the Sierra Madre del Sur, and the three may be sympatric.

### Material Examined

We have seen the type series of *O. atoyac* only; see above for details.

### *Onypterygia shpeleyi*, new species (Fig. 30B, 32C, 33)

#### Type Material

Holotype male, labelled: "MEXICO Gro. 71 km/ne Atoyac de Alvarez/cloud for., 1700 m/beating vegetation/27.07.1992"; "D. Shpeley, H. E. Frania & J. S. Ashe collectors (USNM). Allotype female (USNM) and paratypes five males, three females, labelled same as holotype. Paratypes are distributed as follows: male, female (BMNH); male, female (MNHP); male (CMNC); two males, female (UASM).

#### Type Locality

71 km northeast of Atoyac de Alvarez, Guerrero, Mexico.

#### Specific Epithet

The Latinized genitive form of the surname of the collector of the type series, this name honors Danny Shpeley, Department of Biological Sciences, University of Alberta, in recognition of his substantial contributions in the collection, preparation, analysis, and taxonomic treatment of the Carabidae of the Neotropical region.

#### Diagnostic Combination

With character states of the *O. wappesi* species group, restricted as follows. In addition to character states noted in the key, adults of this species are recognized by a combination of elongate pronotum, sloped elytral humeri, and transverse microsculpture mesh of the elytra. Males are distinguished by form of apex of the median lobe (acuminate in dorsal aspect) and by the armature of the internal sac (single spinose sclerite on the left side, approximately medial in position).

### Description

With diagnostic combination of *O. shpeleyi* and the following.

*Measurements and Proportions of Holotype*.—TL small (7.3 mm), WP/WH low (1.50), LP/WP low (1.00), WP/WPb intermediate (1.50), LE/WE low (1.60).

*Color*.—Head rufous. Antennae with basal articles rufotestaceous; apical articles rufopiceous. Palpi rufous. Pronotum rufous. Elytra with discal pattern concolorous, rufous. Femora, tibiae, and tarsi rufous.

*Microsculpture, Mesh Pattern*.—Elytra, transverse.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae two.

*Prothorax*.—Pronotum (Fig. 30B). Anterior bead incomplete. Lateral margins not sinuate, beaded posteriorly only. Posterolateral pair of setigerous punctures markedly anterad posterolateral angles.

*Pterothorax*.—Mesepisternum impunctate.

*Elytra*.—Elytron, lateral margin narrowly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, moderately deep; punctate for most of length.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—(Fig. 32C) Median lobe, apical portion short; apex acute. Internal sac relatively short; armature, one spinose sclerite.

### Habitat

Specimens were collected in cloud forest, from low vegetation (ca. 1 m high) with vines, the latter forming a tangled mass, with dry leaves suspended on them. A beating sheet was used, about 0.8 m above the ground.

### Geographical Distribution

Known from the type locality only, in the western part of the Sierra Madre del Sur (Fig. 33).

### Chorological Affinities

The locality of this species is close to those for *O. wappesi* and *O. atoyac*, and the three species probably are sympatric.

### Material Examined

We have seen the type series of *O. shpeleyi* only; see above for details.

## *Onypterygia pacifica*, new species (Fig. 17, 32A, 33)

### Type Material

Four specimens. Holotype male, labelled: "MEXICO: Oaxaca/2 miles north/ San Jose Pacifico/July 16, 1974/Clark, Murray/Ashe, Schaffner" (TAMU). Allotype female, labelled same as holotype, except date: "July 20, 1974" (TAMU). Paratype female, labelled: "MEXICO: Oaxaca, 4.6 km/S. Suchixtepec, 2150 m/23.VII.1992 92.023, R. S./Anderson, wet ripar alder/for., leaf litter berlese" (USNM). Paratype male, labelled: "MEXICO: Oaxaca, 10.0 km/S. Suchixtepec, 2000 m/24.VII.1992 92.025, R. S./Anderson, roadside, beating" (CMNC).

### Type Locality

The type locality is 3.2 km north of San José Pacífico, Oaxaca, Mexico.

### Specific Epithet

An adjective, based on part of the Latinized name of the type locality.

### Diagnostic Combination

With character states of the *O. wappesi* species group, restricted as follows. Color rufocastaneous; posterolateral impressions of pronotum small; elytra with striae evanescent, sutural apices angulate, and interval 3 bisetose.

### Description

With diagnostic character states of *O. pacifica* and the following.

**Habitus.**—As in Figure 17.

**Measurements and Proportions of Holotype.**—TL small (7.1 mm), WP/WH low (1.44), LP/WP low (0.88), WP/WPh intermediate (1.38), LE/WE low (1.55).

**Color.**—Head rufous. Antennae with basal and apical antennomeres rufostestaceous. Palpi piceous. Pronotum rufous. Elytra with discal pattern concolorous, bronze; epipleura testaceous, distinctly paler than ventral surface. Femora rufopiceous; tibiae and tarsi rufopiceous.

**Microsculpture, Mesh Pattern.**—Elytra, isodiametric.

**Chaetotaxy.**—Pronotum. Lateral setae two pairs. Elytron, discal setae two.

**Prothorax.**—Pronotum. Anterior bead complete. Lateral margins not sinuate, beaded posteriorly only. Posterolateral pair of setigerous punctures slightly in advance of posterolateral angles.

**Pterothorax.**—Mesepisternum generally punctate.

**Elytra.**—Elytron, lateral margin slightly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 evanescent and punctate for part of length.

**Legs.**—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

**Male Genitalia.**—(Fig. 32A) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; armature, microtrichial patches.

### Habitat

Adults have been collected in leaf litter in wet riparian montane forest, and in roadside vegetation, near such forest.

### Geographical Distribution

This species is known only from the Oaxacan Sierra Madre del Sur (Fig. 33).

### Chorological Affinities

The range of *O. pacifica* does not overlap with the ranges of any other species of the *O. wappesi* species group.

### Material Examined

We have seen the type series of *O. pacifica* only; see above for details.

## The *aeneipennis* Species Group

### Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small in size (TL ca. 7–9 mm); head dorsally and pronotum piceous to black, with hint of green; elytra metallic green or blue, with or without cupreous reflection. Pronotal setae two pairs, each elytron with three discal setae in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and abdominal sternum VII with one pair of posterior marginal setae in males, and two pairs in females. Pronotum (Fig. 34–39) with lateral grooves narrow to moderately broad, lateral margins beaded posteriorly only, or not beaded, sinuate or not posteriorly; posterior pair of lateral setigerous punctures near posterolateral angles, slightly removed from margins, not on bead. Metathorax of average size, not short, metepisternum distinctly longer than wide. Elytral apex rounded, not spined, and sutural apex not angulate or denticulate; interneurs about equally distinct, and preapical lateral calli absent.

### Description

With character states of the *aeneipennis* species group, and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

**Color.**—Body ventrally black to piceous; appendages rufopiceous to rufoflavous.

**Microsculpture.**—Head with microlines fine to effaced more or less extensively, mesh pattern iso-

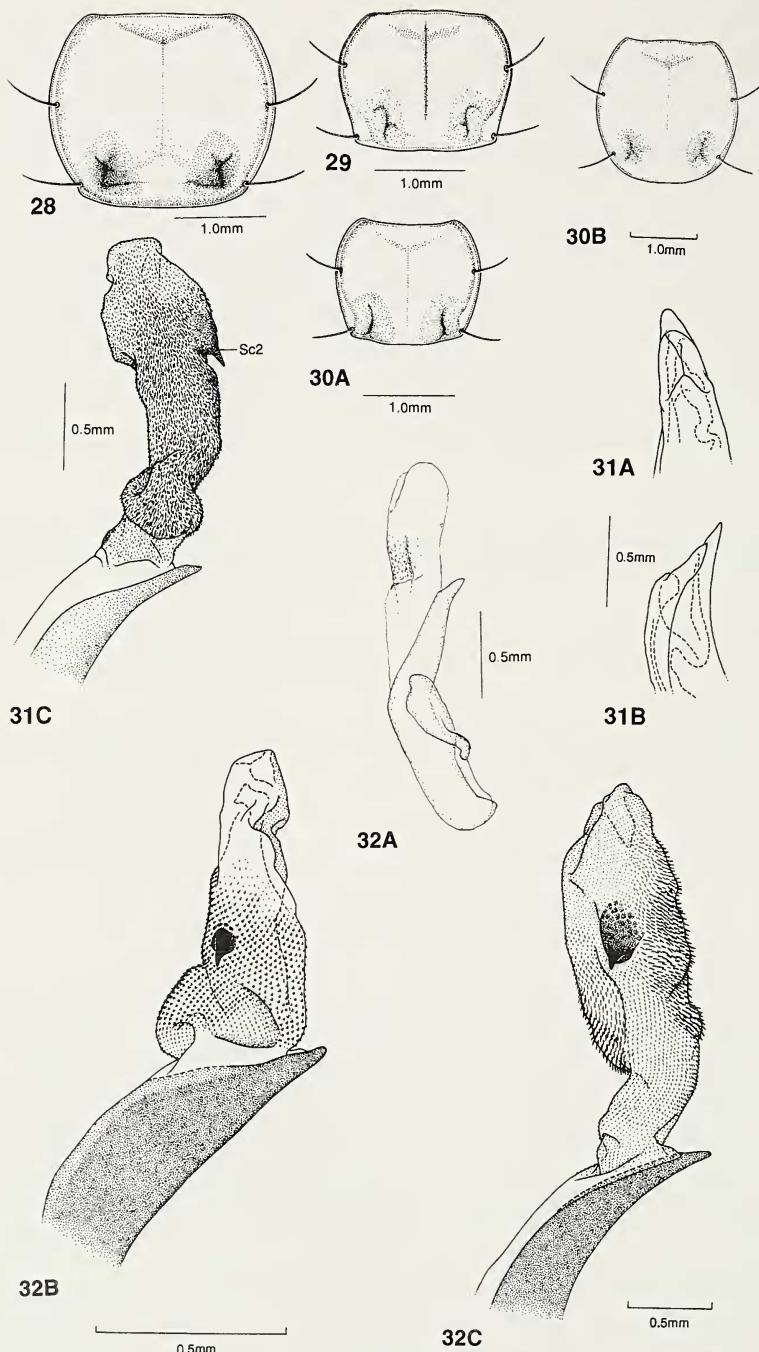


Fig. 28–32C.—Line drawings of adult structural features of the species of the *O. wappesi* species group. Fig. 28–30B, pronotum, dorsal aspect: 28, *O. wappesi*, n. sp.; 29, *O. amecameca*, n. sp.; 30A, *O. atoyac*, n. sp.; 30B, *O. shpeleyi*, n. sp. Fig. 31A–C, male genitalia, *O. wappesi*, n. sp.: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral aspect, with internal sac everted. Fig. 32A–C, median lobe, left lateral aspect, with internal sac everted: A, *O. pacifica*, n. sp.; B, *O. atoyac*, n. sp.; C, *O. shpeleyi*, n. sp. Legend: Sc1, Sc2—spinose sclerites 1 and 2, respectively.

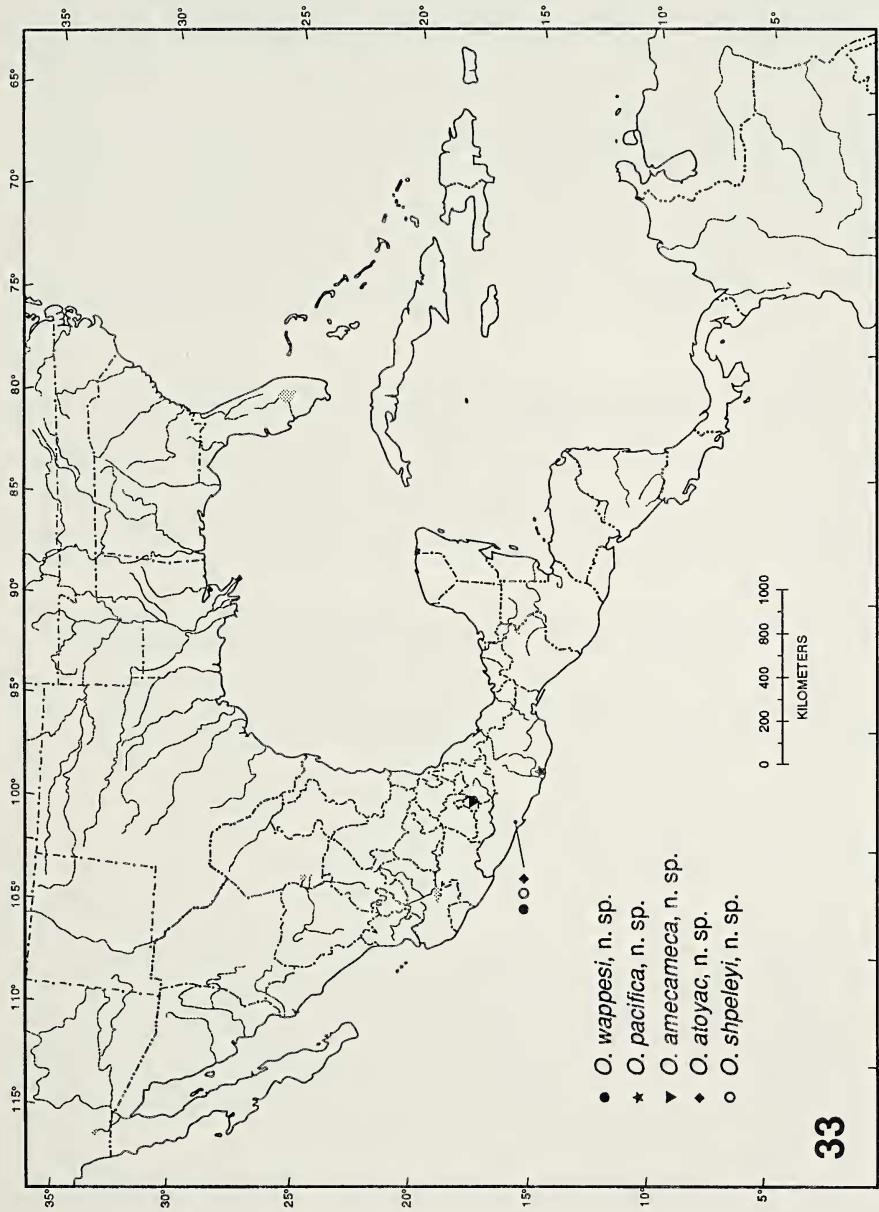


Fig. 33.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the species of the *O. wappesi* species group.

diametric or absent. Pronotum with microlines fine to effaced, mesh pattern transverse or absent. Elytra with microlines distinct, mesh pattern isodiametric to slightly transverse.

*Luster*.—Dorsal surface generally shining.

*Head*.—Frons and vertex smooth, without supraorbital carina each side.

*Prothorax*.—Pronotum (Fig. 34–39), surface sparsely punctate posterolaterally; posterolateral angles prominent to more or less obtuse. Prosternum with intercoxal process rounded apically.

*Elytra*.—Length moderate. Humeri developed fully, rounded. Lateral margins subparallel, slightly rounded. Discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly of equal depth on apical declivity.

*Hind Wings*.—Macropterous, with membrane infuscated, wedge cell elongate, triangular, short sides equal to one another; or brachypterous.

*Legs*.—Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11G:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

*Male Genitalia*.—Median lobe (Fig. 40–45) with apical portion short, triangular, apex narrow; internal sac (Fig. 40C; 41B; 42C; 44C, D; 45) with two spinose sclerites, one basal and one medial, located variously about circumference of internal sac; without basal and preapical lobes.

*Ovipositor*.—Stylomere 2 as in Figure 14, form 1, falcate, with seven or eight lateral ensiform setae, not restricted to dorsolateral margin.

### Taxonomic Notes

All taxa included in this species group are allopatric in relation to one another. They seem to comprise a geographical mosaic entity, and may represent conspecific geographical vicars rather than distinct species. Some samples are brachypterous, others wing-dimorphic, and others macropterous. The metepisternum remains much longer than wide, but is shortened slightly in some populations, and the length of the metasternum between hind and middle coxae is much more than half the length of the hind coxa.

Nearly all geographic samples examined are distinctive, such that possible taxonomic solutions to the group ranged from one geographically varied species to numerous allopatric species. We chose a conservative resolution: since four taxa were named already, we recognize these as valid, and distinguish two others that seem equally distinct. However, since these taxa might be treated by others as subspecies, we discuss them together.

Pronotal variation is extreme. Some samples from the Transvolcanic Sierra (*O. pallidipes*, *O. stenapteryx*) and Sierra Madre del Sur (*O. aeneipennis*, *O. cupri-cauda*) tend to have markedly sinuate lateral margins and sharp posterolateral angles. Other samples from the Transvolcanic Sierra (*O. rubida*) and from various localities in the Sierra Madre Oriental and northern slopes of the Sierra Madre del Sur (*O. batesi*) have the lateral margins barely sinuate and posterolateral angles more obtuse. The pronotal base is notably rounded at sides in specimens from the Sierra Madre Oriental. The width of the lateral grooves varies markedly, from quite narrow in western forms (*O. aeneipennis*, *O. cupri-cauda*, *O. stenapteryx*) to moderately broad in central and eastern taxa (*O. pallidipes* and *O. rubida*, and Sierra Madre Oriental samples of *O. batesi*), and particularly broad in Oaxaca samples of *O. batesi*.

Pterothoracic variation is exhibited by metasternum and metepisternum, by form of elytra, and by development of the hind wings: macropterous specimens have normally developed humeri and a more elongate metepisternum and metasternum; brachypterous specimens have ovate elytra, or at least humeri reduced, and metasternum and metepisternum slightly shortened. *Onypterygia pallidipes* is macropterous, and most specimens have been collected by beating or at lights, at night. The other species are brachypterous or wing-dimorphic, are much less com-

monly collected, and because many specimens have been collected on the ground, the species may be primarily terricolous.

Among the taxa with markedly sinuate lateral pronotal margins, *O. aeneipennis* and *O. cupricauda* seem most similar to *O. stenapteryx*. *Onypterygia pallidipes* is paler (the wider margins of the pronotum, at least, are rufous), but the Uruapan specimen of *O. stenapteryx* also is somewhat pale. If these four nominal forms were assumed to be conspecific, the continuum would be from Oaxaca to Guerrero (medial spinose sclerite of internal sac ventral) to Michoacán to Mexico (spinose sclerite left lateral) to Cuernavaca (spinose sclerite right mediodorsal).

The taxa with slightly sinuate lateral pronotal margins (*O. rubida* and *O. batesi*) are neither proximal nor similar to one another. *Onypterygia rubida* is most similar to *O. pallidipes* although apparently more proximal geographically to *O. stenapteryx*, whereas *O. batesi* is more similar to *O. aeneipennis* and *O. cupricauda* than to the taxa in the Transvolcanic Sierra. The latter similarity involves primarily features postulated to be plesiomorphic.

#### Habitat

The species of the *aeneipennis* group occur in mesic oak, oak-Liquidambar, and oak-pine forest, from about 1000 to 2600 m altitude.

#### Geographical Distribution

The range of this group is confined to central Mexico south of the Tropic of Cancer, extending from the Sierra Madre Oriental in the east, through the Transvolcanic Sierra to the Sierra Madre del Sur on the Pacific Versant (Fig. 46).

#### Chorological Affinities

See "Chorological Affinities" section for *famini* group above.

#### Included Species

The *aeneipennis* species group includes six allopatric species: *O. batesi*, n. sp.; *O. aeneipennis* Chaudoir; *O. cupricauda* Casey; *O. stenapteryx*, n. sp.; *O. pallidipes* Chaudoir; and *O. rubida* Bates.

#### *Onypterygia batesi*, new species

(Fig. 13A, B; 34; 40A-C; 46)

#### Type Material

Sixteen specimens. Holotype male, labelled: "MEX. TAMAULIPAS/Rancho del Cielo/3800', 8 mi. w./Gomez Farias/July 24-29, 1971"; "George E. and Kathleen E. Ball/collectors" (USNM). Allotype female, labelled same as holotype. Fourteen additional paratypes. Male, female, labelled same as holotype. Female, labelled: "MEX. Tamaulipas/Sierra de Guate-/mala, Rancho del/Cielo, 8 mi. n.w./Gomez Farias,/3800' X.6-10.65"; "G. E. Ball/D. R. Whitehead/collectors" (UASM). Three females, labelled: "MEX. S.L.P./24.7 mi. e. Landa/ de Matamoros/ Qro. 9000'/X.18-19.65"; "George E. Ball/D. R. Whitehead/collectors" (BMNH, CUIC, MNHP). Male, labelled: "MEX. QRO. 21.8 km e./Landa de Matamoros/oak, arroyo; 1400 m/20.VIII.1985 63-85"; "MEXICAN EXP. 1985/H. E. Frania & D. Shpeley/collectors" (BMNH). Male, two females, labelled: "MEXICO: Hidalgo/rte. 105, 7.7 km S/Tlanchinol/20 July 1988/R. Turnbow" (RHTC). Male, labelled: "MEXICO: Hidalgo/3.4 km N Tlanchinol/ 21 July 1988/R. Turnbow" (RHTC). Female, labelled: "MEX. Oaxaca/Rte. 190 33.0 mi/n.w. Oaxaca/oak forest/Sept. 4-5, 1967; Ball, T. L. Erwin/R. E. Leech/collectors" (USNM).

tors" (CASC). Female, labelled: "MEX. Oaxaca/Cerro Zempoaltepetl/7200' (below Tla-/huitoltepec)/creek side/August 21, 1972"; "B. S. Heming/G. E. Ball/collectors" (UASM). Female, labelled: "MEX: Veracruz/Las Minas Rd. 10 km/N. Rte 140 29 Jul/1990 el. 1875 m"; "beating/J. K. Liebherr" (CUIC).

#### Type Locality

Rancho del Cielo, Sierra de Guatemala, near Gómez Farías, Tamaulipas, Mexico.

#### Specific Epithet

Latinized genitive form of the surname of Henry Walter Bates; in recognition of his extensive studies of the Neotropical Carabidae.

#### Diagnostic Combination

With character states of *O. aeneipennis* species group, restricted as follows. Femora infuscated; elytra metallic green with evident cupreous reflections laterally, humeri rounded; brachypterous or macropterous; internal sac with distal sclerite ventral; and pronotum moderately broad to broad ( $LP/WP$  0.83–0.94), base moderately to markedly rounded laterally, lateral margins not markedly sinuate before bluntly obtuse posterolateral angles, not beaded, lateral grooves broad, and anterior seta removed from adjacent margin by ca. 1.5–3.0 width of puncture. Adults of this species and *O. pallidipes* differ in that the latter has markedly sinuate pronotal margins (Fig. 38) and noncupreous elytra. In Oaxacan specimens of *O. batesi*, the wide pronotum differs markedly from the narrow pronotum characteristic of *O. aeneipennis*.

#### Description

With diagnostic character states of *O. batesi* and the following.

*Measurements and Proportions of Holotype*.—TL small (7.4 mm), WP/WH intermediate (1.36), LP/WP intermediate (0.91), WP/WPb intermediate (1.24), LE/WE low (1.60).

*Color*.—Antennae with basal and apical articles rufous. Palpi rufopiceous. Pronotum dark green. Femora rufopiceous; tibiae and tarsi rufous.

*Prothorax*.—Pronotum (Fig. 34). Anterior bead complete. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

*Pterothorax*.—Mesepisternum impunctate to generally punctate.

*Elytra*.—Interneurs 2–6 continuous, shallow, punctate for part of length.

*Hind Wings*.—Dimorphic: macropterous or brachypterous.

*Legs*.—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe as in Figure 40A, B. Internal sac (Fig. 40C), armature two spinose sclerites, basal spine dorsal, medial spine ventral.

*Ovipositor*.—Stylomere 2 as in Figure 13A, B.

#### Habitat

Most specimens of this species were taken in terrestrial or creek margin habitats in mesic oak or oak–*Liquidambar* forest, from 1150 to 2200 m altitude, from June through November.

#### Geographical Distribution

This species is known in Mexico from the eastern slopes of the Sierra Madre Oriental, the Transvolcanic Sierra, and Atlantic drainages in Oaxaca (Fig. 46).

#### Chorological Affinities

This species, the only member of the *aeneipennis* species group from Atlantic drainages of the Mexican highlands, is not known to be sympatric with any other members of this group. The most proximal member of the *aeneipennis* group in the Transvolcanic Sierra is *O. pallidipes*.

### *Material Examined*

We have seen the type series of *O. batesi* only; see above for details.

### *Onypterygia aeneipennis* Chaudoir (Fig. 35; 41A, B; 46)

*Onypterygia aeneipennis* Chaudoir (1878:276). Type material: three females, from Oaxaca, Mexico. Lectotype (here designated): first of the three specimens; labelled "Ex Musaeo Chaudoir", Chaudoir—Oberthür collection (MNHP).

*Onypterygia aeneipennis*; Bates, 1882:132.

### *Type Locality*

The type area is "Oaxaca." We restrict the type locality to Santa Catarina Juquila, Oaxaca, Mexico, located on the Pacific Versant of the Sierra Madre del Sur.

### *Diagnostic Combination*

With character states of *O. aeneipennis* species group, restricted as follows. Elytra metallic green with evident cupreous reflections; pronotum narrow (LP/WP 0.95 or more), base moderately rounded laterally, lateral margins markedly sinuate before sharp, nearly right posterolateral angles, beaded posteriorly only, and lateral grooves narrow, with anterior seta removed from margin by about the width of its setigerous puncture; humeri oblique, and hind wings brachypterous. Additionally, males are recognized by the ventral position of the medial sclerite of the internal sac (Fig. 41B).

The pronotum in *O. aeneipennis* adults is much narrower (LP/WP 0.98, two specimens) than in adults of geographically proximal *O. batesi* in Atlantic drainages of Oaxaca (LP/WP 0.83–0.84, two specimens) and *O. cupricauda* in Pacific drainages of Guerrero (LP/WP 0.86–0.89, five specimens). We judge that *O. aeneipennis* is neither sympatric nor continuous with those taxa.

### *Description*

With character states of *O. aeneipennis* and the following.

*Measurements and Proportions*.—TL small (6.65 mm), WP/WH intermediate (1.36), LP/WP intermediate (0.98), WP/WPb intermediate (1.24), LE/WE low (1.56).

*Color*.—Head dark green. Antennae with basal and apical articles piceous-black. Palpi piceous. Pronotum dark green. Elytra bright green. Femora, tibiae, and tarsi piceous-black.

*Prothorax*.—Pronotum (Fig. 35). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

*Pterothorax*.—Mesepisternum partially punctate.

*Elytra*.—Interneurs 2–6 continuous, shallow, completely punctate.

*Hind Wings*.—Brachypterous.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—(Fig. 41A, B) Internal sac, armature (Fig. 41B). Enlarged microtrichia ventral.

### *Geographical Distribution*

The range of this species is confined to the Pacific flanks of the southern part of the Sierra Madre del Sur (Fig. 46). A specimen from Omiltemi, Guerrero, (BMNH) was not examined critically, but may be a member of *O. cupricauda*.

### *Chorological Affinities*

The range of *O. aeneipennis* is isolated from that of its nearest geographical neighbors, *O. batesi* and *O. cupricauda*.

### *Material Examined*

In addition to type material and other specimens of *O. aeneipennis* from the type locality (BMNH and MNHP), we have seen the following, all collected in the Mexican state of Oaxaca.

1 male, 46.7 km S San Pedro Juchatengo, ca 1400 m, X.23.1966, Ray F. Smith (CISC); 1 male, Portillo del Sol, Jalatengo, X.21.1982, H. Brailovsky (CASC); 1 male, 2 females, 40.5 km S Suchixtepec, 1300 m, cloud forest, 92.027, VII.25.1992, R. S. Anderson (UASM).

*Onypterygia cupricauda* Casey  
(Fig. 14; 36; 42A-C; 46)

*Onypterygia cupricauda* Casey (1920:224). Type material: two females (probably collected by Baron).

Lectotype (here designated), female, labelled: "Guer"; "Casey bequest 1919"; "TYPE USNM 47569"; and "cupricauda Cs" (USNM). Paralectotype, female, labelled same as lectotype, except: "cupricauda-2 PARATYPE USNM 47569" (USNM).

#### Type Area

Guerrero, Mexico (probably near Chilpancingo).

#### Type Material

Both Casey specimens have apparently teneral coloration. The paralectotype is macropterous, with metepisternum normally developed and humeri broader than in the lectotype, has deeper interneurs, and its pronotum is relatively narrower anteriorly. As the legs of this specimen are relatively pale, the original description clearly was not based on this specimen.

#### Diagnostic Combination

With character states of the *O. aeneipennis* group, restricted as follows. Elytra metallic green, with marked metallic reflections; pronotum broad (LP/WP 0.86–0.89), base moderately rounded laterally, lateral margins only slightly sinuate before broadly rounded, obtuse posterolateral angles, lateral margins narrow, beaded posteriorly only, and anterior seta removed from margin by about width of its setigerous puncture; and humeri rounded, development average, and hind wings macropterous or brachypterous.

#### Description

With diagnostic combination of *O. cupricauda* and the following.

*Measurements and Proportions*.—TL small (8.0 mm), WP/WH intermediate (1.39), LP/WP intermediate (0.84), WP/WPb intermediate (1.25), LE/WE low (1.50).

*Color*.—Head dark green. Antennae with basal and apical articles rufopiceous. Palpi piceous. Elytra bright green. Femora piceous-black; tibiae and tarsi rufopiceous.

*Prothorax*.—Pronotum (Fig. 36). Anterior bead complete; lateral beads present. Posterolateral impressions densely punctate; angles broadly rounded.

*Pterothorax*.—Mesepisternum generally punctate.

*Elytra*.—Interneurs 2–6 continuous, shallow, punctate for part of length.

*Hind Wings*.—Dimorphic.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—Median lobe as in Figure 42A, B. Internal sac (Fig. 42C), armature two spinose sclerites, median spinose sclerite ventral, preapically and medially with field of slightly enlarged microtrichia.

*Ovipositor*.—(Fig. 14) For details see description of this feature for the *aeneipennis* species group.

#### Habitat

Cloud forest, in vegetation and leaf litter.

#### Geographical Distribution

This species is known only from montane localities on the Pacific slopes of the Sierra Madre del Sur, in Guerrero (Fig. 46). A specimen in BMNH, from Omiltemi, Guerrero, and not examined critically by us, probably belongs to this species.

### *Chorological Affinities*

This species is not known to be sympatric with other members of the *O. aeneipennis* species group, but it is sympatric and perhaps syntopic with *O. wappesi* of the *O. wappesi* species group.

### *Material Examined*

In addition to the type specimens, we have seen 18 specimens from the following localities, all in the state of Guerrero, Mexico.

Nine males, 5 females, 71 km SE Atoyac de Alvarez, cloud for., beating vegetation, 1700 m, 28°9'2", VII.25.1992, D. Shpeley (UASM); 1 male, same locality as above, but collected in tree fall leaf litter, J. S. Ashe (UASM); 1 male, 26 km NW El Paraíso, 1800 m, VIII.9.1986, Rawlins/Davidson (CMNH); 1 male, 1 female, 10 Km WSW Xochipala, 1650 m, VI.30.1982, J. E. Rawlins (CMNH).

### *Onypterygia stenapteryx*, new species

(Fig. 18, 37, 43A–C, 46)

#### *Type Material*

Ten specimens. Holotype male, labelled: "MEX. Michoacán/18.8 mi. w. Uruapan/creek margin/7200'/August 15, 1967"; "Ball, T. L. Erwin/R. E. Leech/collectors" (USNM). Allotype female, labelled: "Tancitaro, Michoacan./MEXICO alt. 6000 ft./June 25 1941 under moss"; "coll H. Hoogstraal"; "Colpodes/sp./det. Val 1942" (USNM). Additional paratypes nine, labelled as follows. Male, "Temascaltepec/Mex. D. F. 1931/G. B. Hinton"; "Van Dyke Collection" (CASC). Two females, "Temascaltepec/1931 Mex. D. F"; G. B. Hinton/Collector"; "Van Dyke/Collection" (CASC). Male, "Bejucos, Mex./Temescaltepec"; "H. E. Hinton/Collector" (MCZC). Male (tips of elytra and terminal abdominal segments missing), "Real de Arriba/Temascaltepec/Mex. VII.1932" (CASC). Female, "MEX: Mich. 14.3 km S/Uruapan, 1370–1465 m/29.vii.88/R. S. Anderson/oak-acacia woodland 88-10" (UASM). Female, "2 mi. NE Ixtapan/de la Sal, Mex., MEX. VII-18-1974/R L Mangan &/D S Chandler" (FSCA). Male, "Harry Brailevsky Col./MEXICO/Halinalco/Edo. de Mé-/xico/19-XI-80"; "Colección del Instituto/de Biología, UNAM./Mexico, D. F"; "♂ gen. drawn/D. Hollingdale/1991" (CASC). Female, "MEX. Mich. 97.7 km/w Apaztingán on rd/to Dos Aguas litter pine-oak; 1700 m/8.VIII.1985 37-85"; "MEXICAN EXP. 1985/H. E. Frania &/D. Shpeley/collectors" (UASM).

#### *Type Locality*

30.2 km west of Uruapan, state of Michoacán, Mexico.

#### *Specific Epithet*

Derived from two Greek words, *stenos* and *pteryx*, meaning narrow winged, with reference to the narrow elytral humeri.

#### *Diagnostic Combination*

With character states of the *O. aeneipennis* species group, restricted as follows. Femora rufous to rufopiceous, and elytra metallic green with cupreous reflections; pronotum broad to narrow (LP/WP 0.85–0.96), base moderately rounded laterally, lateral margins moderately to markedly sinuate anterad sharply obtuse postero-lateral angles, lateral margins narrow, beaded posteriorly only, and anterior seta removed from margin about 1.0–1.5 width of its setigerous puncture; elytral humeri oblique, hind wings brachypterous. Further, males are distinguished by the left-lateral position of the medial spinose sclerite of the internal sac.

### Description

With diagnostic character states of *O. stenapteryx* and the following.

**Habitus.**—As in Figure 18.

**Measurements and Proportions of Holotype.**—TL small (6.62 mm), WP/WH intermediate (1.28), LP/WP intermediate (0.93), WP/WPb intermediate (1.28), LE/WE low (1.52).

**Color.**—Head dark green. Antennae with basal and apical articles rufous. Palpi rufopiceous. Elytra bright green. Femora piceous-black; tibiae and tarsi rufopiceous.

**Prothorax.**—Pronotum (Fig. 37). Anterior bead complete; lateral beads present. Posterolateral im-pressions impunctate, or sparsely punctate; angles obtuse.

**Pterothorax.**—Mesepisternum impunctate, or partially punctate.

**Elytra.**—Interneurs 2–6 continuous, moderately deep, or shallow; impunctate, or punctate for part of length.

**Hind Wings.**—Brachypterus.

**Legs.**—Tarsomeres 1–3 of middle tarsi sulcate; tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

**Male Genitalia.**—Median lobe as in Figure 43A, B. Internal sac (Fig. 43C) with enlarged micro-trichia few, ventral.

### Variation

The Uruapan specimen, which seems to be fully mature, is paler than other specimens. The Ixtapan specimen has bluish elytra, clearly green and with cupreous reflections only near apex. Pronotal form varies considerably: LP/WP 0.92 at Ixtapan, 0.88–0.96 at Temascaltepec, 0.93 at Uruapan, 0.85 at Apatzingán, and 0.86 at Tancítaro. The Tancítaro specimen has the lateral margins of the pronotum less markedly sinuate and posterolateral angles more obtuse.

### Habitat

Specimens have been collected on the ground in pine–oak litter, along a creek margin, and in moss. The known altitudinal range is from 1700 to 2200 m.

### Geographical Distribution

This species is known from the southern fringes of the Transvolcanic Sierra in the central Mexican states of México and Michoacán (Fig. 46).

### Chorological Affinities

Known localities of *O. stenapteryx* are on portions of the Río Balsas system that drain the southern slopes of the Transvolcanic Sierra. Other taxa in the *O. aeneipennis* species group that therefore may be continuous or sympatric with *O. stenapteryx* are *O. rubida* and *O. pallidipes*.

### Material Examined

We have seen the type series of *O. stenapteryx* only; see above for details.

### *Onypterygia pallidipes* Chaudoir (Fig. 38, 44A–D, 46)

*Onychopterygia pallidipes* Chaudoir, 1878:276. Holotype male, labelled: “TYPE/H.T.” [circular, ringed with red]; “Puebla”; “Mexico/ Sallé Coll.”; “614”; “Type”; “B.C.A. Col.I.1/ Onypterygia / pallidipes,/ Chaud;” “Onypterygia/ pallidipes/ Chaud/ Puebla” [handwritten]; “Onychopterygia/ pallidipes Chaud/ apud Sallé” [handwritten]; “Holo-/ type” [circular, ringed with red]; ♂ BMNH/HOLOTYPE/ det. D. R. Whitehead/ Onypterygia/ pallidipes/ Chaudoir/ det. D. R. Whitehead” (BMNH).

*Onypterygia pallidipes*; Bates, 1882:132.

### Type Material

Chaudoir (1878:276) records but a single specimen of this species, from the collection of A. Sallé. Thus, we infer that, in the absence of a specimen of this

species in the MNHP from the Sallé Collection, the one noted above must be the one on which Chaudoir based his description.

#### Diagnostic Combination

With character states of the *O. aeneipennis* species group, restricted as follows. Pronotum with lateral margins pale, femora rufous, and elytra rufescent with metallic green or blue cast but with little or no apical cupreous reflections; pronotum moderately broad ( $LP/WP$  0.83–0.92), base straight laterally, lateral margins markedly sinuate anterad obtuse to acute posterolateral angles, lateral margins broad, not beaded, and anterior seta removed from side margin by about 2.0 width of its setigerous puncture; humeri broadly rounded, and hind wings macropterous. Further, males are distinguished by the medial spinose sclerite of internal sac being right mediodorsal in position.

Males are similar to those of *O. rubida* in lacking cupreous elytral color and by having the medial sclerite of the internal sac dorsal, but differ from that species by the markedly sinuate lateral margins of the pronotum and by the acute posterolateral angles. In elytral color, a specimen of *O. stenapteryx* from the geographically proximate locality of Ixtapan de la Sal is transitional in elytral color to *O. pallidipes*.

#### Description

With diagnostic character states of *O. pallidipes* and the following.

*Measurements and Proportions*.—TL small (7.45 mm), WP/WH intermediate (1.33), LP/WP intermediate (0.92), WP/WPb intermediate (1.22), LE/WE low (1.47).

*Color*.—Head dark green. Antennae with basal and apical antennomeres rufotestaceous. Palpi testaceous. Elytra bright green. Femora, tibiae, and tarsi rufotestaceous.

*Prothorax*.—Pronotum (Fig. 38). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles acute.

*Pterothorax*.—Mesepisternum impunctate, or partially punctate.

*Elytra*.—Interneurs 2–6 continuous, shallow; impunctate, or punctate for part of length.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–3 of middle tarsi sulcate; tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—Median lobe as in Figure 44A, B. Internal sac (Fig. 44C, D) moderately long; enlarged microtrichia ventral.

#### Habitat

This species lives in tropical deciduous and oak forests, at altitudes between 1400 and 2100 m. Adults have been collected in June, July, and August: at night, at UV light traps, and in daytime by beating low vegetation.

#### Geographical Distribution

This species occurs on the southern edge of the Transvolcanic Sierra of the central Mexican states of Morelos and Puebla (Fig. 46).

#### Chorological Affinities

This species is not known to be sympatric with others of the *O. aeneipennis* species group, but may be continuous with *O. stenapteryx* and *O. rubida*, which also live on the southern slopes of the Transvolcanic Sierra drained by the Río Balsas.

#### Material Examined

In addition to the type specimen, we have seen approximately 25 specimens of *O. pallidipes* in total. All localities are in Mexico.

**Morelos:** Cuernavaca (UASM); 7 and 8.7 km E Cuernavaca (CASC, USNM, UASM). **Puebla:** 7 km SE Chipilo (UASM); Puebla (BMNH).

*Onypterygia rubida* Bates  
(Fig. 39, 45, 46)

*Onypterygia rubida* Bates 1884:286. Type material: possible holotype, teneral male, H. W. Bates—Oberthür Coll. (MNHP).

*Type Locality*

Pátzcuaro, Michoacán, Mexico.

*Diagnostic Combination*

With character states of the *O. aeneipennis* species group, restricted as follows. Pronotum with lateral margins pale, femora rufous, elytra rufescent with metallic blue or green cast, and no apical cupreous reflections; pronotum moderately broad (LP/WP 0.87–0.89), base nearly straight to moderately curved laterally, lateral margins very slightly sinuate anterad broadly to markedly obtuse posterolateral angles, lateral margins broad, beaded posteriorly only, and anterior seta removed from lateral margin by about 1.5–2.0 width of its setigerous puncture. Further, males are distinguished by the medial spinose sclerite of the internal sac being dorsal in position.

*Description*

With character states of *O. rubida*, and the following.

*Measurements and Proportions*.—TL small (7.42 mm), WP/WH intermediate (1.31), LP/WP intermediate (0.89), WP/WPB intermediate (1.25), LE/WE low (1.57).

*Color*.—Head rufopiceous. Antennae with basal and apical antennomeres rufostaceous. Palpi testaceous. Pronotum rufopiceous. Elytra bright blue. Femora, tibiae, and tarsi rufostaceous.

*Prothorax*.—Pronotum (Fig. 39). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

*Pterothorax*.—Mesepisternum impunctate, or partially punctate.

*Elytra*.—Interneurs 2–6 continuous, moderately deep, impunctate, or punctate for part of length.

*Hind Wings*.—Dimorphic.

*Legs*.—Tarsomeres 1–3 of middle tarsi sulcate. Tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—Internal sac moderately long, with enlarged microtrichia in broad mediopreapical band (Fig. 45).

*Habitat*

Adults have been collected on the ground, in pastures, in August, from altitudes of 2130 to 2590 m.

*Geographical Distribution*

This species is known from the Transvolcanic Sierra, from the Mexican states of Michoacán and Colima (Fig. 46).

*Chorological Affinities*

The range of this species may be continuous with those of *O. pallidipes* and *O. stenapteryx*, related species that also live on the southern slopes of the Transvolcanic Sierra drained by the Río Balsas.

*Material Examined*

In addition to the type, we have seen three specimens of *O. rubida*, all from Mexico, as follows.

**Colima:** 1 male, 5–10 km S Mazamitla, X.6.1992, J. E. Wappes (JEWC). **Michoacán:** Huajumbaro (UASM); E Morelia (UASM); Pátzcuaro (BMNH).

The *perissostigma* Species Group

*Diagnostic Combination*

With character states of *Onypterygia*, restricted as follows. Adults of this species group are recognized readily by the very narrow, elongate body form (Fig.

19). Other features are: body size small (TL ca. 8 mm), color testaceous to rufotestaceous, elytra with metallic green reflection; frons and vertex each side with pronounced longitudinally directed carina; with two pairs of lateral pronotal setae, each elytron with three discal setae in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with five to six pairs. Metepisternum distinctly longer than wide. Elytron with apex rounded, not spined, sutural apex not denticulate; surface without preapical lateral calli.

### Description

With diagnostic combination of *perissostigma* species group, restricted as follows. Body slender, pronotum elongate, measurements and proportions as in Table 2.

**Color.**—Testaceous to rufotestaceous, head and pronotum with dorsal surfaces rufoaeneous, elytra with metallic green reflection; antennae, palpi, and legs testaceous.

**Microsculpture.**—Head and pronotum smooth, without microlines. Elytra with microlines fine, mesh pattern isodiametric.

**Luster.**—Dorsal surface generally shining.

**Chaetotaxy.**—Pattern indicated in “Diagnostic Combination” section above.

**Head.**—Eyes markedly convex, prominent.

**Prothorax.**—Pronotum (Fig. 47) with surface posterolaterally densely punctate, especially in and around posterolateral impressions; anterior bead complete, lateral margins sinuate posteriorly and narrowly beaded; lateral grooves narrow; posterior setigerous puncture each side close to distinct posterolateral angle, slightly removed from margin, not on bead. Prosternum with intercoxal process truncate apically.

**Pterothorax.**—Mesepisternum generally punctate. Metathorax normal size, metepisternum distinctly longer than wide.

**Elytra.**—Narrow, elongate. Elytron with humerus broadly rounded; lateral margin straight; discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly, on apical declivity, of equal depth; interneurs punctate for part of length. For other details see “Diagnostic Combination” section above.

**Hind Wings.**—Macropterous, with wedge cell elongate, triangular, with short sides in length equal to one another.

**Legs.**—Tarsomeres 1–3 of middle and hind tarsi sulcate laterally. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe longer than basal portion (Fig. 11C:l-4). Tarsomere 5 with ventrolateral setae thin, short, and few (Fig. 11D:vs); tarsomeres 2–4 with relatively few climbing setae (Fig. 11C). Tarsal claws with pectinations less extensive (Fig. 11E:p).

**Male Genitalia.**—Median lobe (Fig. 48) with apical portion short, apex narrow. Internal sac with one or more microtrichial fields, without basal and preapical lobes, setiform spines, and spinose sclerites.

**Ovipositor.**—Stylomere 2 form 1, falcate, with ca. 15–16 ensiform setae on dorsolateral margin and on lateral surface generally.

### Habitat

The single included species is in montane tropical forest, at an altitude of 609 m. Although a locality as low as this one may seem hardly “montane,” according to the Holdridge system, vegetation formations in Middle America occurring as low as 500 m are classified as montane (Hartshorn, 1988). More specifically, the forest of the area in question was designated by Sarukhan (1968:14, fig. 4) as “Selva alta-mediana subperennifolia” and distinguished from lowland rain forest or “Selva alta perennifolia.” This distinction was not made by Rzedowski (1978: 159), who combined these forest types in one unit, designated “Bosque Tropical Perennifolio.” Because so few species of *Onypterygia* are known to enter true lowland tropical forest, we choose to follow the classifications of Hartshorn and Sarukhan rather than Rzedowski for characterization of habitats of this genus.

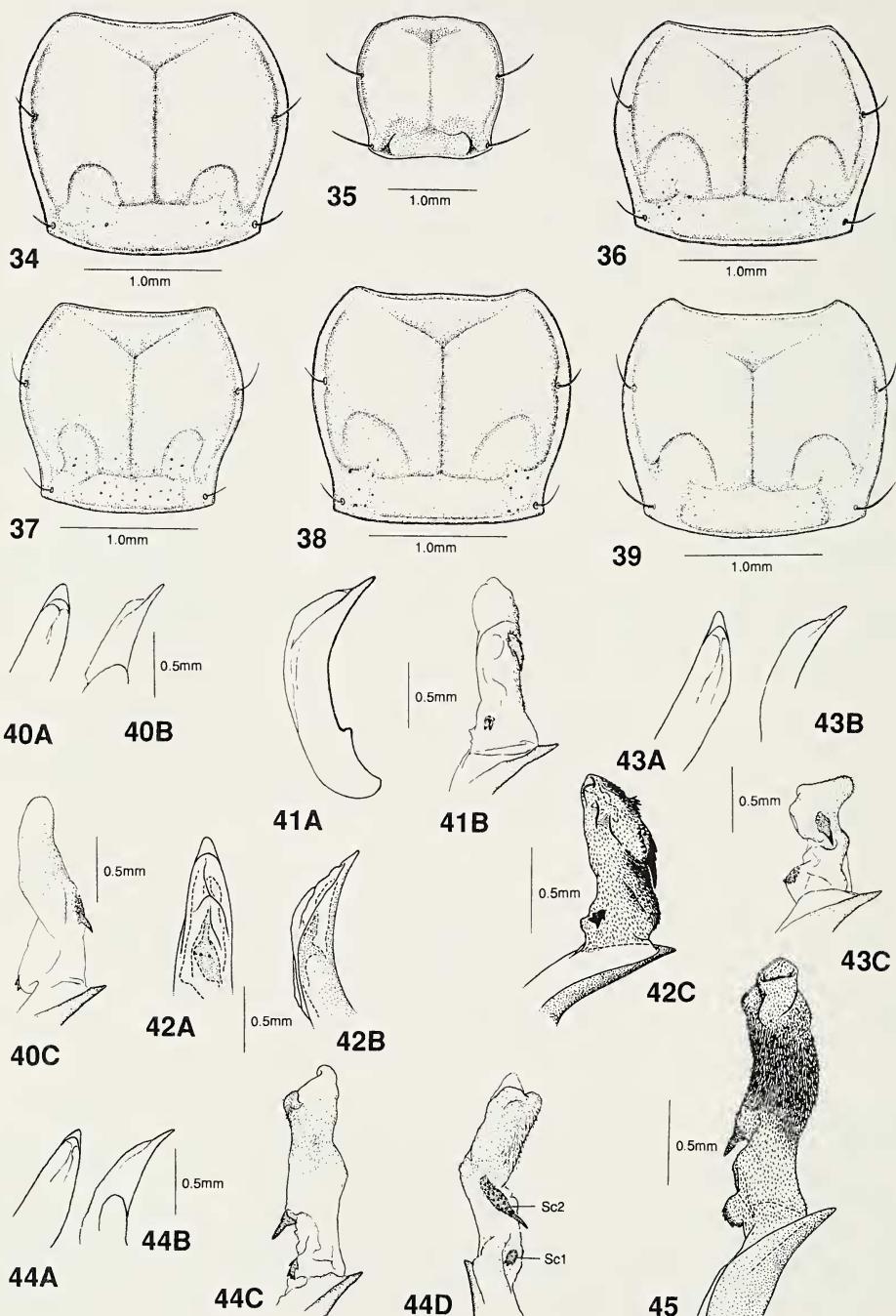


Fig. 34–45.—Line drawings of adult structural features of the species of the *O. aeneipennis* species group. Fig. 34–39, pronotum, dorsal aspect of: 34, *O. batesi*, n. sp.; 35, *O. aeneipennis* Chaudoir; 36, *O. cupricauda* Casey; 37, *O. stenapteryx*, n. sp.; 38, *O. pallidipes* Chaudoir; 39, *O. rubida* Bates. Fig. 40–45, male genitalia of: 40, *O. batesi*, n. sp.; A, B, median lobe, apical portion, dorsal and left lateral aspects respectively; 41, *O. aeneipennis* Chaudoir, median lobe; A, left lateral aspect; B, median lobe; 42, *O. stenapteryx*, n. sp., median lobe; A, left lateral aspect; B, median lobe; 43, *O. pallidipes* Chaudoir, median lobe; A, left lateral aspect; B, median lobe; C, apical portion, dorsal aspect; 44, *O. cupricauda* Casey, median lobe; A, left lateral aspect; B, apical portion, dorsal aspect; C, median lobe, dorsal aspect; D, median lobe, left lateral aspect; 45, *O. rubida* Bates, median lobe.

### Geographical Distribution

This species is known from Mexico only, in central Oaxaca (Fig. 52).

### Chorological Affinities

See "Chorological Affinities" section for the *famini* species group above.

### Included Species

This group is monobasic, including only *O. perissostigma*, n. sp.

### *Onypterygia perissostigma*, new species (Fig. 11C–E; 19; 47; 48; 52)

#### Type Material

Four specimens. Holotype male, labelled: "2000', 6 mi. S./Valle Nacional./Oax. Mex. V.18–20/1971 H. Howden" (USNM). Allotype female, labelled same as holotype (USNM). Two additional paratypes, labelled as follows. Female, labelled same as holotype (BMNH). Female, "MEX. Oaxaca, 16.9/mi. S. Valle/Nacional 3600'/VIII.14–15.65"; "George E. Ball/D. R. Whitehead/collectors"; "pn drawn" (UASM).

#### Type Locality

9.7 km south of Valle Nacional, Oaxaca, Mexico.

#### Specific Epithet

Based on two Greek words, *perissos* and *stigma*, meaning oddly marked, in reference to the densely punctate pronotum as peculiar to this species.

#### Description

*Habitus*.—As in Figure 19.

*Measurements and Proportions of Holotype*.—TL small (7.50 mm), WP/WH high (1.04), LP/WP high (1.16), WP/WPb low (1.16), LE/WE high (1.96). See group description above for other details.

*Pronotum*.—As in Figure 47.

*Legs*.—Tarsal claws as in Figure 11C–E.

*Male Genitalia*.—As in Figure 48.

#### Variation

Paratypes vary in amount of genal rugosity; they are more fully matured than the holotype, and hence the elytra are darker beneath the metallic green luster.

#### Habitat

One of the paratypes (UASM) was collected near the margin of a temporary woodland pond in montane rain forest, as were specimens of *O. kathleenae*. Moth scales on their integument indicate that the holotype and other paratypes were collected at light.

### Geographical Distribution

This species is known only from the eastern slopes of the continental divide, in central Oaxaca (Fig. 52).

←

apical portion, with internal sac everted. 42, *O. cupricauda* Casey: A, B, median lobe, dorsal and left lateral aspects, respectively; C, internal sac everted, left lateral aspect. 43, *O. stenapteryx*, n. sp.: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, internal sac everted, left lateral aspect. 44, *O. pallidipes* Chaudoir: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, D, internal sac, everted, left and right lateral aspects, respectively. 45, *O. rubida* Bates: median lobe, apical portion, with internal sac everted. Legend: Sc1—spinose sclerite 1, Sc2—spinose sclerite 2.

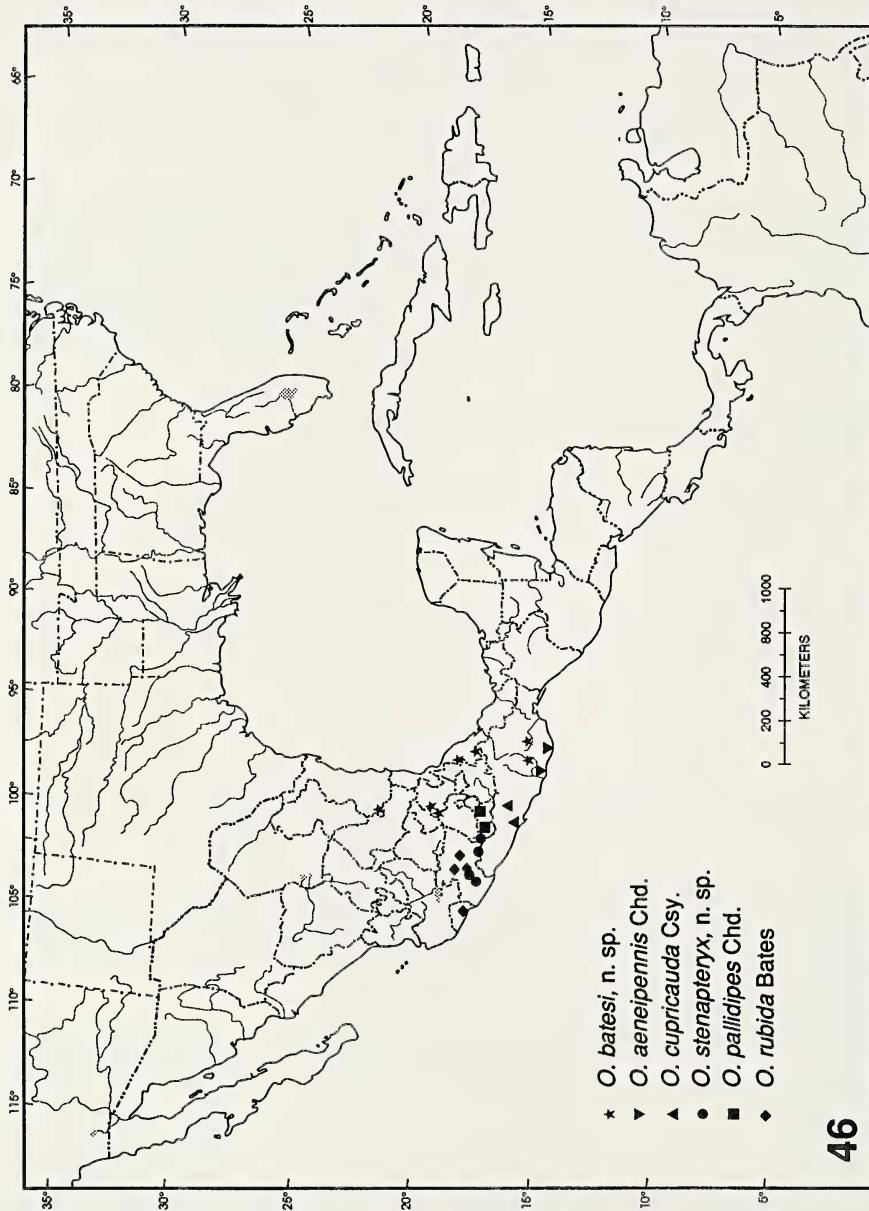


Fig. 46.—Map of southern North America, Middle, and northern South America showing collecting records for the species of the *O. aeneipennis* species group.

### *Chorological Affinities*

This species is sympatric with *O. kathleenae* in Oaxaca. Localities of *O. strigblingi* and *O. exeueros* are in close proximity to that of *O. perissostigma*, so it seems likely that these species are sympatric. Also, the ranges of most other species groups overlap that of *O. perissostigma*, so one can expect reasonably that additional species will be sympatric with *O. perissostigma*.

### *Material Examined*

We have seen the type material of *O. perissostigma* only; for details see above.

### The *pusilla* Species Group

#### *Diagnostic Combination*

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small (TL ca. 7–9 mm), head dorsally and pronotum piceous to black, elytra with disc concolorous, metallic green with cupreous reflection laterally to dark aeneous, with only a bare trace of color. Pronotal lateral setae two pairs, each elytron with three discal setae, in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with single pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with two pairs. Elytral apex produced and angulate or denticulate (Fig. 49C), sutural apex rounded, interneurs about equally distinct, and preapical lateral elytral calli absent.

#### *Description*

With diagnostic combination of *pusilla* species group and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

**Color.**—Body generally dark rufopiceous; palpi, tibiae, and tarsi paler, rufous; antennae with basal antennomeres piceous, apical antennomeres piceous to rufopiceous; elytra as noted in “Diagnostic Combination” section above.

**Microsculpture.**—Head nearly smooth, without microlines, or microlines very few and mesh pattern isodiametric. Pronotum with microlines very fine, surface nearly smooth, mesh pattern transverse. Elytra with microlines distinct, mesh pattern isodiametric.

**Luster.**—Dorsal surface shining.

**Head.**—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

**Prothorax.**—Pronotum as in Figure 49A, B, sparsely punctate posterolaterally, posterolateral angles obtuse; anterior bead complete; lateral margins slightly sinuate posteriorly, beaded posteriorly only, lateral grooves moderately wide; posterolateral pair of setigerous punctures at posterolateral angles, slightly removed from margin, not on bead. Prosternum with intercoxal process rounded apically.

**Pterothorax.**—Mesepisternum partially punctate. Metathorax normal, metepisternum distinctly longer than wide.

**Elytra.**—Humeri broadly rounded; lateral margins slightly rounded, subparallel; discal and umbilical setigerous punctures deep, not foveate; interneurs 1 and 2 equally distinct posteriorly, on apical declivity; interneurs 2–6 continuous, moderately deep, punctate for part of length.

**Hind Wings.**—Macropterous, with membrane hyaline, not darkened; wedge cell elongate, triangular, with short sides equal to one another.

**Legs.**—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe shorter than basal portion. Tarsomeres 2–4 with climbing setae markedly dense (cf. Fig. 11F). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11D). Tarsal claws with pectinations more extensive (cf. Fig. 11H).

**Male Genitalia.**—Median lobe (Fig. 50A–E) with apical portion short, triangular, apex narrow; internal sac (Fig. 50C) without basal or preapical lobes; relatively short, with single basal spinose sclerite, or without spinose sclerites.

**Ovipositor.**—Stylomere 2 (cf. Fig. 51) form 1, falcate, with eight to ten ensiform setae on or near dorsolateral margin.

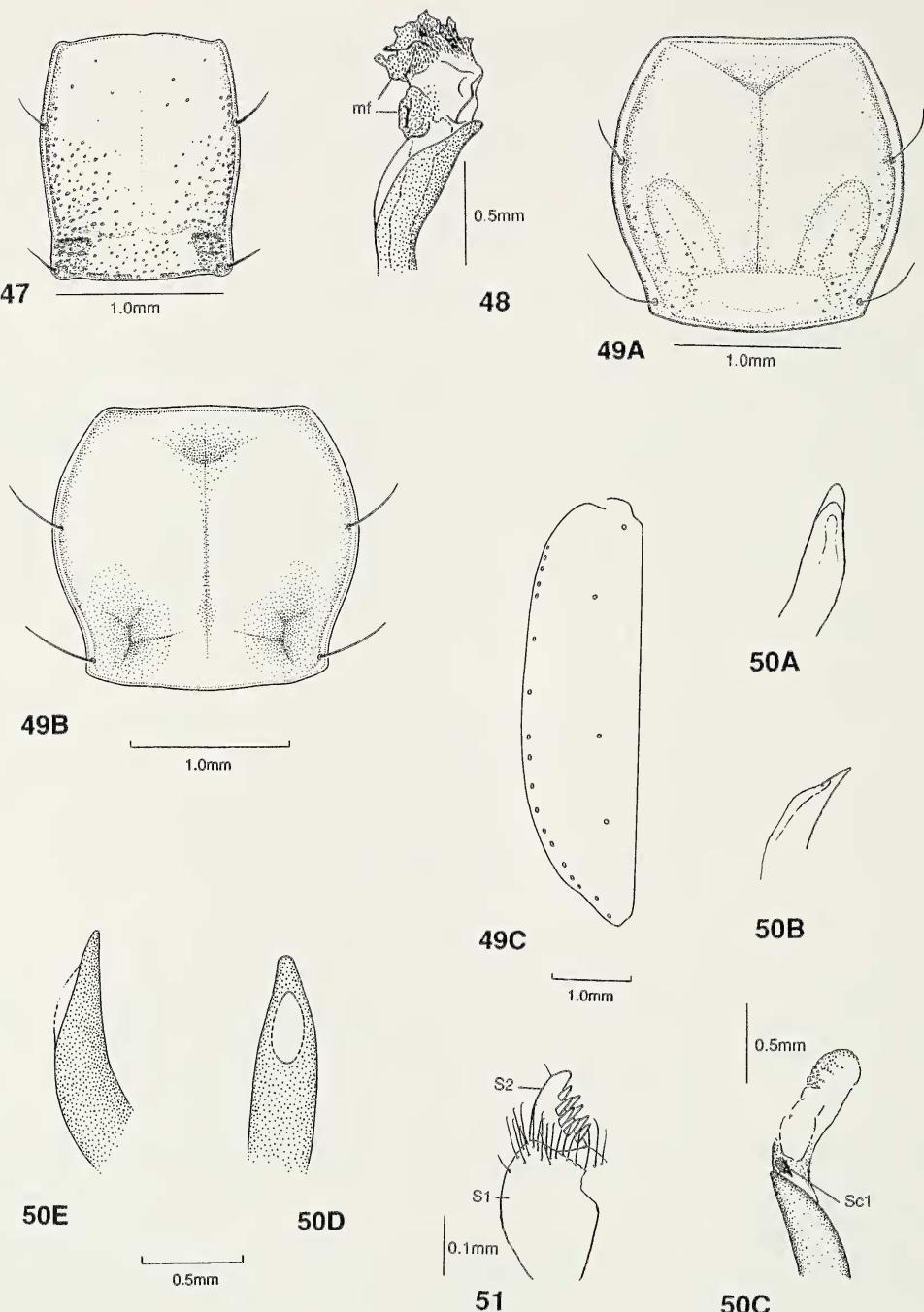


Fig. 47-51.—Line drawings of adult structural features of the *O. perissostigma* and *O. pusilla* species groups. Fig. 47, 49A, 49B, pronotum, dorsal aspect of: 47, *O. perissostigma*, n. sp.; 49A, *O. pusilla* Chaudoir; 49B, *O. rawlinsi*, n. sp. Fig. 49C, left elytron, dorsal aspect, of *O. rawlinsi*, n. sp. Fig. 48, 50, male genitalia: 48, *O. perissostigma*, n. sp., median lobe, apical portion, left lateral aspect, with internal sac everted; 50A-C, *O. pusilla* Chaudoir: A, B, median lobe, apical portion, dorsal and left

### Habitat

The species of this group are known from tropical montane and oak-pine forests, between 700 and 1800 m altitude.

### Geographical Distribution

The range of this species group is bicentric, with one species occurring on the Pacific Versant of Mexico in the southern part of the Sierra Madre Occidental and adjacent Transvolcanic Sierra, and another one farther south in the eastern Transvolcanic Sierra, Sierra Madre del Sur, and in the mountains of Chiapas and Guatemala (Fig. 52).

### Chorological Affinities

See "Chorological Affinities" for *famini* group above.

### Included Species

This group includes two species: *O. pusilla* Chaudoir, and *O. rawlinsi*, n. sp.

#### *Onypterygia pusilla* Chaudoir (Fig. 49A, 50A–C, 51, 52)

*Onychopterygia pusilla* Chaudoir 1878:276. Lectotype (here designated) male, with green Dejean labels "pusilla in Mexico" and "Orizaba"; also "Ex Musaeo Chaudoir" (Oberthür-Chaudoir Collection, Box 293/2/4, MNHP).

*Onypterygia pusilla*; Bates, 1882:133.

### Type Material

In addition to the specimen noted above, Chaudoir (1878:277) referred to other specimens in the collection of Auguste Sallé, from Córdoba. These are designated paralectotypes.

### Type Locality

Orizaba, Veracruz, Mexico.

### Diagnostic Combination

With character states of *O. pusilla* species group, restricted as follows. Elytral apices angulate, color of elytra dull, nonmetallic to slightly metallic, and elytral interneurs relatively deeply engraved.

### Description

With diagnostic combination of *O. pusilla* and the following.

*Measurements and Proportions*.—TL small (7.70 mm), WP/WH high (1.33), LP/WP intermediate (1.18), WP/WPb intermediate (1.21), LE/WE high (2.00).

*Color*.—Elytra metallic green with coppery reflections laterally. Legs with femora piceous-black; tibiae and tarsi rufopiceous.

*Prothorax*.—Pronotum (Fig. 49A).

*Elytra*.—Elytron, apex angulate to denticulate or acuminate.

*Male Genitalia*.—Median lobe as in Figure 50A, B. Internal sac (Fig. 50C), armature, one spinose sclerite.

*Ovipositor*.—Stylomere 2 as in Figure 51.

←

lateral aspects, respectively; C, median lobe, apical portion, with internal sac everted; D, E, *O. rawlinsi*, n. sp., median lobe, dorsal and left lateral aspects, respectively. Fig. 51, ovipositor, stylomeres 1 and 2, lateral aspect, of *O. pusilla* Chaudoir. Legend: mf—microtrichial fields; S1, S2—stylomeres 1 and 2, respectively; Sc1—spinose sclerite 1.

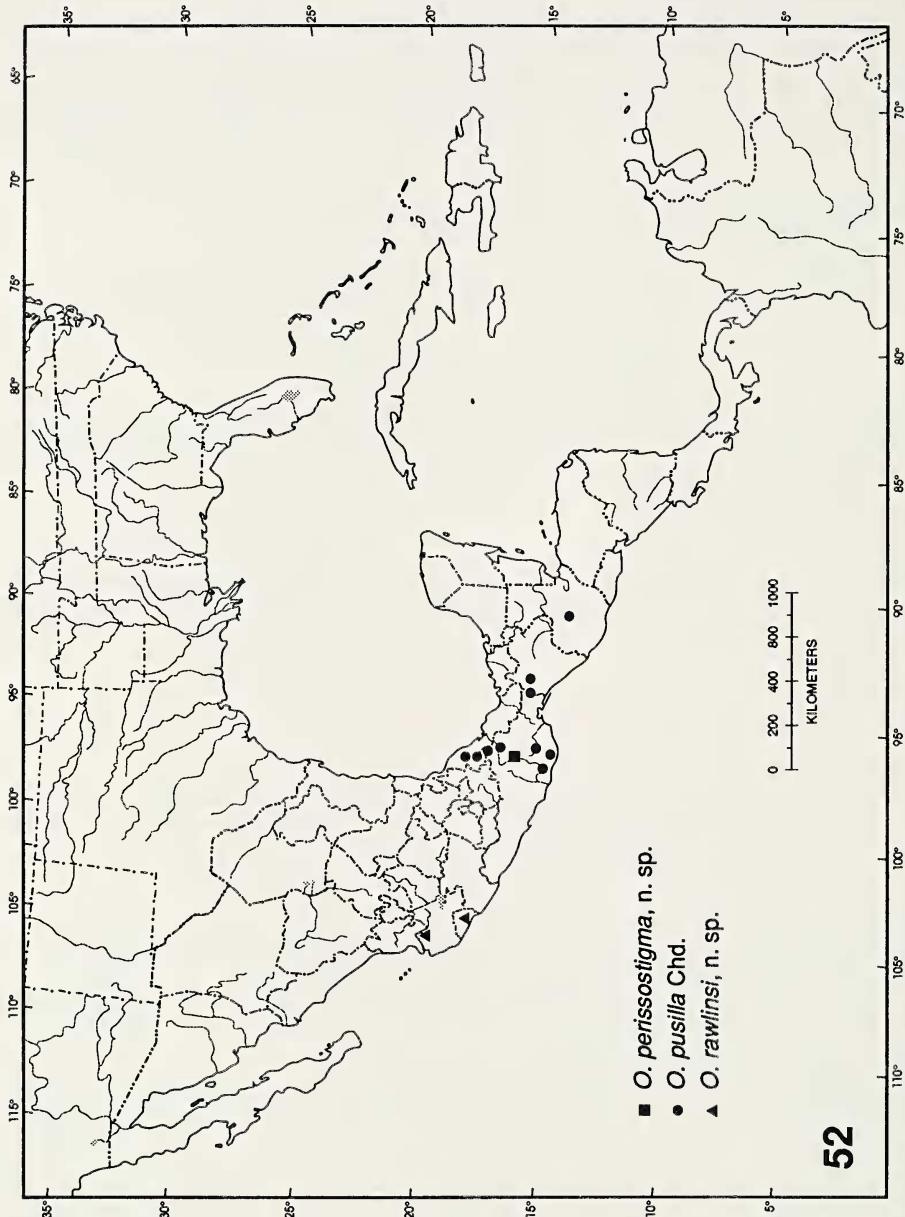


Fig. 52.—Map of southern North America, Middle, and northern South America showing positions of collecting records for the *O. perissostigma* and *O. pusilla* species groups.

### Variation

A male from San Gabriel Mixtepec, Oaxaca, exhibits acuminate elytral apices, the projections almost as long and slender as those characteristic of *O. longispinis* Bates.

### Habitat

Mexican specimens were collected in mesic woodlands at middle altitudes (884–1372 m): from bromeliads in March and December, at UV light traps in June, and by other methods from May through September.

### Geographical Distribution

The range of this species extends from Guatemala northward in the west to the Sierra Madre del Sur in Oaxaca, and in the east to Jacala, in the state of Hidalgo (Fig. 52).

### Chorological Affinities

This species is allopatric in relation to its closest relative, *O. rawlinsi*, n. sp. At Suchixtepec, Oaxaca, adults of *O. pusilla* were collected from bromeliads with adults of *O. angustata* and *O. hoepfneri*.

### Phylogenetic Relationships

This species and *O. rawlinsi*, n. sp., are postulated to be adelphotaxa.

### Material Examined

In addition to the type material we have seen approximately 70 specimens of *O. pusilla* from the following localities.

**MEXICO.** **Chiapas:** 10 km SW Ocósingo, 1067 m, VII.29.1966, Ball and Whitehead (UASM); 2 males, 10.3 km NW Ocósingo, 1069 m, oak–pine woodland, VII.19.1983, R. S. Anderson (UASM); 18.7 km N Ocozocoautla, 975 m, U-V light, VI.10–13.1966, Ball and Whitehead (UASM); Jct. Rts. 190 & 195, VI.11.1969, J. M. Campbell (CNCI). **Distrito Federal:** Mexico City. **Hidalgo:** 1 female, 46.7 km NE Jacala, 1371.6 m, V.27.1974, Marshall, C. W. & L. O'Brien (UASM); 1 female, 46.7 km NE Jacala 1372 m, V.27.1979, C. W. & L. O'Brien & B. Marshall (UASM). 46 km. SE Tamazunchale, 1494 m, VI.4.1975, Ball and H. E. Frania (UASM). **Oaxaca:** 1 specimen, 8 km S Candelaria Loxicha, VII.18–19.1974 (TAMU); 1 specimen, Juquila Mixes, V., H. F. Howden (CNCI); 3 males, Hwy. 131, 193 km S Oaxaca, 1463 m, V.12.1971, D. E. Bright (CNCI); 3 males, 1 female, Rte. 131, 187 km S Oaxaca, 1768 m, V.12.1971, J. M. Campbell (CNCI); Puerto Escondido Highway—52–58 km N Puerto Escondido (UASM); 1 specimen, 30.7 km S Suchixtepec, 1372 m, in bromeliads, Ball and Whitehead (UASM); 1 female, 11 km S Valle Nacional, 610 m, V.8.1971, D. E. Bright (CNCI); 2 males 3 females, 24 km S Valle Nacional, 1219 m, V.20.1971, D. E. Bright (CNCI); 5 specimens, 9.7 km S Valle Nacional, 610 m, V.18–20.1966, Ball and Whitehead (UASM); 1 specimen, 19.4 km S Valle Nacional, 914 m, V.17.1966, Ball and Whitehead (UASM); 1 specimen, 24 km S Valle Nacional, 1219 m, V.20.1966, Ball and Whitehead (UASM). **Veracruz:** 5 specimens, Córdoba (CASC); 8 specimens, same locality, VI.9–11, VII.8 (USNM); 1 specimen, Fortín de las Flores, 884 m, U-V light, V.27–28.1966, Ball and Whitehead (UASM); 6 km S Huatusco, 1370 m, cloud forest, bromeliads, VII.20.1978, G. E. and K. E. Ball (UASM); 1 female, Hwy. 140, 7.1 km N. Huatusco, 1300 m, beating weeds and vines, J. K. Liebherr, D. A. Millman (CUIC); Jalapa. 2 females, 1 km N. Jilotepec, 1300 m, beating, VII.31.1990, J. K. Liebherr (CUIC); Orizaba; 1 male, Río Metlac, 4 km S Fortín de las Flores, 900 m, VII.17.1990, J. K. Liebherr (CUIC). **GUATEMALA.** **Alta Verapaz:** 3 specimens, Panzós (BMNH, MCZC, Nègre Coll., MNHP); 1 female, San Cristóbal Quixal, V.I.1980, H. & L. Freude (ZSMC); 1 specimen, Senahú (BMNH). **Baja Verapaz:** 1 male, 7 km NE Purulhá, 1660 m, tropical montane forest, beating vegetation, 91-08, V.31.1991, Howden Exp., D. Shpeley, & K. E. & G. E. Ball (UASM).

### *Onypterygia rawlinsi*, new species (Fig. 49B; 50D, E; 52)

#### Type Material

Fourteen specimens, as follows. Holotype male, labelled: “23 km S Tepic,/Nayarit MEXICO/3500' July 17/1977 J. Rawlins” (CMNH). Allotype female and

additional paratypes (five males and five females) labelled same as holotype (CMNH, UASM). Two additional paratypes, labelled: male, "MEXICO Colima/ vic El Terrero/4 Oct 1992/R. Turnbow"; "Los Sauces rd./km mk. 1-2" (RHTC). Female, "MEXICO Colima W./Rd. to El Terrero/3-5000 ft. 3-5 Oct/1992 J. E. Wappes" (JEWC).

#### Type Locality

Mexico, state of Nayarit, 23 km south of Tepic.

#### Specific Epithet

This is the Latinized genitive form of the surname of the collector of most of the type series, John E. Rawlins, lepidopterist and Associate Curator, Section of Invertebrate Zoology, Carnegie Museum of Natural History, and named in recognition of and with gratitude for his enthusiastic efforts to improve knowledge of Neotropical Carabidae.

#### Diagnostic Combination

With character states of *O. pusilla* species group and, in addition to the distinctive combination of character states presented in the key, males of this species are recognized by absence of spinose sclerites from the internal sac of the genitalia. In size, form, and color, adults of *O. rawlinsi* are confused easily with those of the *O. aeneipennis* species group, but they differ in form of elytral apex: broadly rounded in the latter, obtusely angulate in the former.

#### Description

With diagnostic combination of *O. rawlinsi*, and the following. Body form and size average for the more primitive lineages of *Onypterygia*.

*Measurements and Proportions of Holotype*.—TL small (7.16 mm), WP/WH high (1.39), LP/WP intermediate (0.98), WP/WPb intermediate (1.32), LE/WE high (1.71).

*Color*.—Elytra aeneous. Legs, tibiae, and tarsi piceous to black.

*Prothorax*.—Pronotum as in Figure 49B.

*Male Genitalia*.—(Fig. 50D, E) Internal sac, armature absent.

#### Habitat

Probably rather dry oak-pine forest, to judge from the general vegetation cover in the areas where the specimens were collected. In fact, the specimens were taken at a light trap set "amid cornstalks at the edge of a small milpas . . ." and "the . . . forest nearby was disturbed secondary growth . . ." (John Rawlins, personal communication).

#### Geographical Distribution

This species is known only from the western slopes of the Sierra Transvolcanica in Mexico (Fig. 52).

#### Chorological Affinities

Specimens of this species were collected at the same time and in the same place as were specimens of *O. cyanea* and *O. hoepfneri*. This species is clearly isolated from the range of its putative adelphotaxon, *O. pusilla*, but it is overlapped by the species of the *O. aeneipennis* group, as well as being syntopic with the species noted above.

#### Phylogenetic Relationships

See this topic for *O. pusilla* above.

#### Material Examined

We have seen the type series of *O. rawlinsi* only; see above for details.

### The *angustata* Species Group

#### *Diagnostic Combination*

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small to intermediate in size (TL 7–11 mm), head dorsally and pronotum piceous to black, elytra with disc concolorous, metallic green, with cupreous reflection laterally, or completely cupreous. Pronotal lateral setae, one or two pairs, each elytron with three setae in or near interval 3, hind femur with or without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, and females with two pairs. Elytral apex denticulate to acuminate (spinose), sutural apex angulate or rounded, interneur 1 more deeply impressed than other interneurs, and each elytron with a preapical lateral callus (Fig. 54C).

#### *Description*

With diagnostic combination of *angustata* species group, and the following.

*Measurements and Proportions*.—As in Table 2.

*Color*.—Body and appendages (except elytra) black to rufopiceous; see “Diagnostic Combination” section above for color of elytra.

*Microsculpture*.—Head with dorsal surface smooth, microlines absent, or mesh pattern partially effaced only, sculpticells isodiametric. Pronotum with surface nearly smooth, but microlines evident in small patches, mesh pattern transverse. Elytra with microlines fine, mesh pattern isodiametric.

*Luster*.—Dorsal surface shining.

*Head*.—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

*Prothorax*.—Pronotum (Fig. 53; 54A, B), with surface smooth to densely punctate posterolaterally; posterolateral angles nearly rectangular; anterior margin with bead complete; lateral margins slightly sinuate posteriorly, beaded posteriorly only; lateral grooves moderately wide; posterolateral pair of setigerous punctures at posterolateral angles on or beside bead. Prosternum with intercoxal process rounded apically.

*Pterothorax*.—Mesepisternum impunctate to partially punctate. Metathorax normal, metepisternum distinctly longer than wide.

*Elytra*.—Moderately elongate. Elytron with humerus broadly rounded; lateral margin slightly rounded; discal setigerous punctures foveate or not; umbilical punctures foveate or not. Interneurs fine, interneur 1 posteriorly on apical declivity much deeper than interneur 2; interneurs 2–6 continuous, fine, punctate for part of length, or impunctate. Other details in “Diagnostic Combination” section, above.

*Hind Wings*.—(Fig. 55) Macropterous, wedge cell oblong, with short sides unequal to one another.

*Legs*.—Tarsomeres 1–2 or 1–3 of middle and hind tarsus sulcate laterally. Fore tarsomere 4 with inner lobe as long as or longer than basal part; hind tarsomere 4 with outer lobe shorter than, or as long as, basal portion. Climbing setae of tarsomeres 2–4 markedly dense (cf. Fig. 11F, G:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

*Male Genitalia*.—Median lobe (Fig. 56–59) with apical portion short, triangular, apex narrow; internal sac (Fig. 56C, 57C, 59B) moderately elongate, without basal or preapical lobes, with basal spinose sclerite only, or with basal and median spinose sclerites.

*Ovipositor*.—Stylomere 2 (Fig. 60, 61) form 1, falcate, with four to ten ensiform setae on or near dorsolateral margin.

#### *Habitat*

The species of this group occupy mesic tropical montane to oak–pine forests, from about 600 to 1900 m altitude.

#### *Geographical Distribution*

The range of this group extends from Mexico south of the Tropic of Cancer to Panama and possibly to northern South America (Fig. 62).

#### *Chorological Affinities*

See “Chorological Affinities” for *famini* group above.

### *Included Species*

Four species are included in this group: *O. longispinis* Bates; *O. angustata* Chevrolat; *O. pseudangustata*, n. sp.; and *O. striblingi*, n. sp.

### *Onypterygia longispinis* Bates (Fig. 10, 56A-C, 62)

*Onypterygia longispinis* Bates, 1882:132. Lectotype (here designated) male on card with female, labelled "TYPE H. T."; "Cerro Zunil, 4-5000 ft. Champion"; "Onypterygia longispinis Bates" [handwritten]; "B.C.A. COL. I.1. Onypterygia longispinis Bates" (Drawer 361/5/2, BMNH).

### *Type Locality*

Here restricted to Cerro Zunil, Quetzaltenango, Guatemala.

### *Diagnostic Combination*

With character states of the *O. angustata* species group, restricted as follows. Elytra with marked aeneous cast, pronotum with both pairs of marginal setae, and elytral apices markedly acuminate (Fig. 10).

### *Description*

With diagnostic combination of *O. longispinis* and the following.

*Measurements and Proportions*.—(Topotype female) TL intermediate (10.4 mm), WP/WH intermediate (1.49), LP/WP low (0.90), WP/WPb intermediate (1.26), LE/WE intermediate (1.77).

*Prothorax*.—Pronotum. Posterolateral impressions impunctate, or sparsely, shallowly punctate.

*Pterothorax*.—Mesepisternum partially punctate.

*Elytra*.—Elytron (Fig. 10), lateral margin narrowly rounded, not sinuate. Sutural apex rounded, or angulate. Interneurs 2-6 punctate for part of length. Discal setigerous punctures not foveate.

*Legs*.—Tarsomeres 1-3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—(Fig. 56A-C) Internal sac, armature one spinose sclerite.

### *Variation*

Specimens from Panzós, Sinanja, and Sabo have proportionately longer elytral spines and tend to be more purplish than those from Cerro Zunil and Tacaná.

### *Habitat*

This species inhabits vegetation in montane tropical and humid to dry oak-pine forests, between 1300 and 1900 m altitude.

### *Geographical Distribution*

This species is known from Guatemala and adjacent parts of Chiapas, in Mexico (Fig. 62).

### *Chorological Affinities*

The range of *O. longispinis* is overlapped by the range of *O. angustata*, also of the *O. angustata* species group, and by the ranges of various species of the *O. famini*, *pusilla*, and *fulgens* groups. Additional details are provided below, under "Ecological Aspects."

### *Material Examined*

We have seen about 75 specimens of *O. longispinis* from the following localities in Mexico and Guatemala.

**MEXICO. Chiapas:** Chincultic (Ruinas) on road to Montebello: 1 male, VIII.29.1982, Clark & Cave (AUEM); 1 female, VI.12.1989, H. F. Howden (UASM). Lagunas (or Lagos) de Montebello: 1 male, M. J. & C. A. Tauber (CUIC); 1 male, Cinco Lagos, 1500 m, oak-pine-Liquidambar forest, ix.21.1991, R. S. Anderson (CMNC); 3 males, 1 female, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 1 male, Laguna Pojoj, 1500 m, VI.2.1990, H. & A. Howden (UASM); 1 female, Sumidero de Río Comitán, 1372 m, VIII.31.1974, D. E. & J. A. Breedlove (CASC); 1 male, Municipio Tenejapa,

Paraje Kulaktik, 1524 m, X.9.1981, D. E. Breedlove, C. G. Whitfield (CASC); Volcán Tacaná, 1524 m, bromeliads, XII.21 (UASM). **GUATEMALA.** **Alta Verapaz:** Panzós (MCZC). **Baja Verapaz:** 1 male, 5.2 km W Chilascó, 1650 m, oak–pine forest, V.24.1991, R. S. Anderson (CMNC); 3 females, 9.6 km W Chilascó, 1560 m, humid oak–pine forest, U–V light, 91–21, V.30.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 1 female, same, 91–21, V.24.1991 (UASM); 1 female, 5.5 km W Cobán rd., from Pantin Jct., 1620 m, dry oak forest, beating vegetation, 91–17, V.31.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 2 males, 1 female, Pantin Rd., 3 km S Cobán Hwy, 1600 m, VI.6.1993, H. & A. Howden (UASM); 1 male, 6–9 km E Purulhá, IV.15–16.1990, J. E. Wappes (JEWC); 3 males, 8 km S Purulhá, 1660 m, tropical montane forest, UV light, 91–05, V.19.1991, Shpeley, Ball & Ball (UASM); 2 males, 1 female, same, V.20.1991 (UASM); 1 male, 7 km NE Purulhá, 1500 m, VI.5.1993, H. & A. Howden (UASM); 2 males, 1 female, 14.5 km S Purulhá, 1600 m, tropical montane forest, beating vegetation, 91–13, V.21.1991, Shpeley, Ball & Ball (UASM); Sabo (BMNH, MCZC, USNM); 1 male, 1 female, 17.5 km N. Salamá (on #5), 1650 m, oak–pine forest, 93–38, VII.3.1993, R. S. Anderson (CMNC); 1 male, 19–24 km N. Salamá, 1372 m, V.25–31.1989, J. E. Wappes (JEWC). Sinanja (BMNH). **Quetzaltenango:** Cerro Zunil (BMNH, MCZC, USNM). **Zacapa:** 4 males, 2 females, Sierra de las Minas, 20.3 km N. Tecolutan, 1800–1900 m, tropical montane forest, beating, 91–34, VI.8.1991, Shpeley, Ball & Ball (UASM); 1 male, nr. San Lorenzo, 1219–1829 m, IV.13.1990, J. E. Wappes (JEWC).

*Onypterygia angustata* Chevrolat  
(Fig. 53, 55, 57A–C, 60, 62)

*Onypterygia angustata* Chevrolat, 1835:160. Lectotype (here designated), male with posterior end of abdomen damaged by dermestid, labelled: "Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909, E. B. Poulton."; "TYPE COL: 149 Onypterygia angustata Chevr. HOPE DEPT. OXFORD" (OXUM).—Bates, 1882: 132 (in part).

*Onychopterygia angustata*; Gemminger and Harold, 1868:384 (invalid emendation). Chaudoir, 1878: 276.

*Type Locality*

Cruz Blanca, Veracruz, Mexico.

*Diagnostic Combination*

With character states of *O. angustata* species group, restricted as follows. Pronotum with two pairs of lateral setae, posterolateral angles of pronotum not sparsely punctate, elytron with apex in form of an obtuse angle, and interneurs finely but distinctly punctate. In Mexico, *O. angustata* and *O. pseudangustata* are the only small (length less than 12 mm) species in the genus with a denticulate elytral apex. In the vicinity of Jalapa, Veracruz, where these species are sympatric, *O. angustata* differs by having both pairs of lateral marginal setae and distinctly punctulate elytral interneurs; also, most individuals are smaller, with the pronotum more narrowed basally, and the elytra coppery rather than green. In Costa Rica, the elytral apices of *O. angustata* tend to be only slightly angulate.

*Description*

With diagnostic combination of *O. angustata* and the following.

*Measurements and Proportions*.—(Male, Jalapa, Veracruz) TL small (7.9 mm), WP/WH intermediate (1.33), LP/WP low (1.00), WP/WPb low (1.18), LE/WE intermediate (1.74).

*Color*.—Antennae with basal and apical antennomeres piceous to black, or rufopiceous. Palpi piceous. Elytra with disc bronze-green, metallic. Femora, tibiae, and tarsi piceous to black, or rufopiceous.

*Chaetotaxy*.—Pronotum, lateral setae two pairs.

*Prothorax*.—Pronotum (Fig. 53). Posterolateral impressions sparsely punctate.

*Pterothorax*.—Mesepisternum partially punctate.

*Elytra*.—Elytron, lateral margin narrowly rounded, not sinuate. Apex acuminate, spine shorter; sutural apex rounded. Interneurs 2–6 impunctate. Discal setigerous punctures not foveate.

*Hind Wings*.—Venation as in Figure 55.

*Legs*.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—(Fig. 57A–C). Internal sac, armature two spinose sclerites.

*Ovipositor*.—Left stylomeres 1 and 2 as in Figure 60.

### Habitat

Adults were collected in montane tropical, and mesic oak–pine forests, between 1000 and 2300 m altitude. Many specimens were taken from bromeliads, most others by beating vegetation.

### Geographical Distribution

The known range of *O. angustata* extends from Panama northward to central Veracruz, in eastern Mexico (Fig. 62).

### Chorological Affinities

This species is sympatric, at least in part, with *O. famini*, *O. pusilla*, *O. longispinis*, *O. fulgens*, *O. tricolor*, and *O. hoepfneri*.

### Material Examined

We have seen 222 specimens of *O. angustata* from the following localities. Some were intercepted at U. S. ports of entry with various plants, including orchids, from Guatemala, Honduras, Mexico, and Nicaragua.

**MEXICO.** **Chiapas:** 2 females, Chincultic, VIII.29.1982, Clark & Cave (AUEM); 1 male, El Sumidero, 1000 m, X.21.1988, R. Turnbow (RHTC); 1 female, same, V.25.1990, H. & A. Howden (UASM); 48 & 54 km N. Huixtla (UASM); Pueblo Nuevo, 5 & 35 km S Pueblo Nuevo (UASM); 2 females, 14.3 km S Tapilula, 1463 m, cloud forest, VII.7.1983, R. S. Anderson, W. Maddison (UASM); 1 male, 1 female, Volcán Tacaná, Union Juárez, NE slope Barranca Providencia, 1600 m, montane tropical forest, ex vegetation overhanging road cut, XII.24–25.1975, H. E. Frania and J. Belicek (UASM); 16 males, 9 females, Volcán Tacaná, 1524 m, ex bromeliads, XII.21.1976, H. E. Frania, D. L. C. Proctor (UASM). **Colima:** 1 male, 14 km E Minatitlán, VII.17.1990, J. E. Wappes (JEWJC). **Distrito Federal:** 1 specimen, from Mexico City, intercepted with orchids (USNM). **Hidalgo:** 2 females, Rte. 105, 7.7 km S Tlanchinol, VII.20.1988, R. Turnbow (RHTC). **Jalisco:** 1 specimen, Sebastián, Sierra Madeiro Mts., 1800 m, II.1 (CASC). **Michoacán:** 1 female, Tingambato, XI.20.1980, H. Brailovsky (CASC). **Oaxaca:** Juquila (BMNH); Juquila Mixes, V.1971, M. S. Miller (CNCI); 3 specimens, 55.5 km N. Pochutla, III.19–20.1966, Ball and Whitehead (UASM); 2 specimens, 30.7 km S Suchixtepec, in bromeliads, III.17.1966, Ball and Whitehead (UASM). **Puebla:** 1 female, Xicotepetec de Juárez, VII.13.1980, H. Brailovsky (CASC). **Veracruz:** Córdoba (BMNH); 5 males, 3 females, 3.9 km NE Coscomatepec, 1310 m, in bromeliads on acacias, 78B-26, XI.19.1978, G. E. & K. E. Ball (UASM); 11.6 km NE Coscomatepec, bromeliads (UASM); 1 male, Hwy. 140, 7.1 km N. Huatusco, 1300 m, beating weeds & vines, VIII.15.1987, J. K. Liebherr, D. A. Millman (CUIC); 20 specimens, 16.7 km SW Huatusco, 1433 m, in bromeliads, III.8.1966, Ball and Whitehead (UASM); 1 male, Jalapa, Instituto de Ecología, 1300 m, ex epiphytes, XI.25.1994, Purrington & C. Drake (FFPC); 1 female, Jalapa, La Pitahaya, 1300 m, ex epiphytes, XII.1.1994, Purrington & C. Drake (FFPC); 1 male, 3 km S Jalapa, 1350 m, V.25–30.1991, B. Ratcliffe, J. Ashe, M. Jameson (SEMC); 1 female, 1 km N. Jilotepec, beating, 1300 m, VII.31.1990, J. K. Liebherr (CUIC). 1 specimen, Metlac, in bromeliads, XII (FSCA). **BELIZE.** **Toledo:** Sarstoon River (BMNH). **COSTA RICA.** **Cartago:** 2 specimens, Cervantes, 1450 m, IV.8 (USNM); 5 specimens, Tres Ríos (MCZC). **Puntarenas:** 5 specimens, Coronado, on blossom “plomillo,” V.23 (USNM); 1 female, Monteverde, 1372 m, V.21–26.1979, J. M. & B. A. Campbell (CNCI); 1 male, same, 1500 m, II.26.1991, K. M. Hamilton (UASM); 1 male, same, H. & A. Howden (UASM). **San José:** 2 specimens, San José, II.3, XI.2 (USNM). **EL SALVADOR.** 1 female, Cerro Verde, V.1.1971, H. F. Howden (UASM). **La Libertad:** 2 specimens, Volcan El Boquerón (Nègre Coll., MNHP). **Santa Ana:** 1 specimen, Hidalgo Montecristo, Metapán, 2300 m, cloud forest (FSCA). **GUATEMALA.** **Baja Verapaz:** 1 male, 8.6 km W Chilascó, 1560 m, VI.7.1993, U-V light, H. & A. Howden (UASM). **Chimaltenango:** 2 specimens, S. P. Yepocapa, 1463 m, sweeping, V.10, light, V.12 (FMNH); 1 specimen, same (USNM). **El Progreso:** 5 males, 6 females, 20 km N. Estancion de la Virgen, 1900 m, cloud forest, VI.8.1991, R. S. Anderson (CMNC); 1 male, 21 km N. Estancion de la Virgen, 1829 m, VI.3.1991, J. E. Wappes (JEWJC). **Escuintla:** 1 male, 4 km N. Palín, VI.21.1966, J. M. Campbell (CNCI). **Guatemala:** 3 males, Guatemala City, 1 km SE La Pueblito, 1700 m, oak scrub forest, VI.11.1991, R. S. Anderson (CMNC); 1 male, 4 females, same, 1850 m, oak–pine forest, beating vegetation, 91-37, VI.10.1991, Shpeley, Ball & Ball (UASM); 2 males, 5 females, Guatemala City, Universidad del Valle campus, 1511 m, oak–pine forest, 91-36, VI.10.1991, Shpeley, Ball & Ball (UASM); 15 males, 9 females, Puente Parada, 14.5 km SE Guatemala City, 1790

m, oak-pine forest, beating vegetation, 91–41, VI.13.1991, Shpeley, Ball & Ball (UASM); 2 females, same, A. Howden (UASM). **Jalapa:** 1 female, Mataquescuintla, Finca Concepción, VII.2.1986, J. M. Campbell (CNCI). **Sacatepéquez:** Capetillo (BMNH); 1 male, 4.5 km NW San Miguel Dueñas, 1760 m, VI.12.1991, H. & A. Howden (UASM). **Zacapa:** 2 females, 19 km N. Estacion del Virgen, 1219 m, IV.18–21, 1990, J. E. Wappes (JEW); 1 female, Sierra de las Minas, San Lorenzo, 1740 m, VII.18.1986, J. M. Campbell (CNCI); 7 males, 7 females, Sierra del Espíritu Santo, 3 km SE La Union, 1400–1500 m, U-V light, 91–31, VI.6.1991, Shpeley, Ball & Ball (UASM). **HONDURAS.** **Federico Morazán:** 1 female, 37 km E Tegucigalpa, VIII.8.1982 (TAMU); 2 females, Cerro Uyuca, 30 km E Tegucigalpa, 1800 m, V.16.1994, H. & A. Howden (UASM); 2 males, 2 females, V.19.1994 (UASM); 1 female, V.30.1994 (UASM); 1 specimen, near Tegucigalpa, intercepted with plants, II (FSCA); 1 male, 1 female, 6 km SE Zamorano, 850 m, U-V light, H. & A. Howden (UASM). **Intibuba:** 1 female, 6 km W La Esperanza, XII.3.1995, R. H. Turnbow (RHTC). **Olancho:** 5 males, 12 females, Parque Nacional La Muralla, at MV + UV light, V.24–VI.12.1995, R. H. Turnbow (RHTC); 1 male, 2 females, same locality, XI.29.1995, R. H. Turnbow (RHTC). **Paraíso:** 1 male, 4 females, Cerro Montserrat, 7 km SW Yuscarán, 1800 m, V.21.1994, H. & A. Howden (UASM); 1 male, 4–7 km SE Danli, XI.29.1995, R. H. Turnbow (RHTC). **NICARAGUA.** 1 male, 20 km N. Matagalpa, VII.1989, F. Reinholdt (UNAN); 1 specimen, "Nicaragua," intercepted with plants XI (FSCA). **PANAMA.** **Chiriquí:** 1 male, 1 female, Bambito, S. Cerro Punta, 1585 m, IV.23.1976, M. S. Carter & C. L. Molineux (CASC); 1 female, 3 km W Cerro Punta, 8°51'N, 82°36'W, 1720 m, XI.26.1976, H. P. Stockwell (UASM); Volcán de Chiriquí (BMNH).

### *Onypterygia pseudangustata*, new species (Fig. 54A; 58A, B; 59A, B; 61, 62)

Bates, 1882:132 (as *O. angustata* Chevrolat).

#### *Type Material*

Fifteen specimens, labelled as follows. Holotype male, labelled: "6 mi. East/Teziutlan, Pueb MEX./VII.4–6,60/H. F. Howden" (CNCI). Allotype female, labelled: "Jalapa/Mexico/Hoege" (BMNH). Thirteen paratypes, as follows. Male, labelled same as holotype. Nine, labelled same as allotype. Male and female, labelled: "Jalapa/Mexico/Hoege"; "Ex/Godman/and/Salvin" (MCZC). Male, labelled: "5 mi. N./Teziutlan, Pue./27.VI.1975 MEX.;" "J. E. Gillaspy/Collector" (CUIC).

#### *Type Material*

Bates (1882:132) included the Hoege specimens noted above in his series of *O. angustata*.

#### *Type Locality*

9.7 km east of Teziutlán, Puebla, Mexico.

#### *Specific Epithet*

Two words, Greek, *pseudo-*, meaning false, and Latin, *angustata*, the name of another species of *Onypterygia*. Together, they mean "false-angustata," in allusion to the similarity and sympatry of, and past confusion with, *O. angustata*.

#### *Diagnostic Combination*

With character states of *O. angustata* species group, restricted as follows. Pronotum with a single pair (posterolateral) of lateral setae and elytral apex angulate, but not acuminate. Compared to adults of *O. angustata*, those of *O. pseudangustata* are larger on average, with the pronotum less narrowed posteriorly, the elytra green rather than coppery, the preapical lateral elytral calli more prominent, and the elytral interneurs deeper and much less distinctly punctulate.

#### *Description*

With diagnostic combination of *O. pseudangustata*, and the following.

*Measurements and Proportions of Holotype.*—TL small (9.0 mm), WP/WH intermediate (1.56), LP/WP low (0.84), WP/WPb intermediate (1.25), LE/WE intermediate (1.73).

*Color.*—Antennae with basal and apical antennomeres piceous to black. Palpi piceous. Elytra with disc metallic green. Femora, tibiae, and tarsi piceous to black.

*Prothorax.*—Pronotum (Fig. 54A). Posterolateral impressions densely punctate.

*Pterothorax.*—Mesepisternum impunctate.

*Elytra.*—Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Sutural apex rounded. Interneurs 2–6 punctate for part of length. Discal setigerous punctures foveate.

*Legs.*—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia.*—(Fig. 58A, B; 59A, B) Internal sac (Fig. 59B), armature two spinose sclerites on right side.

### *Geographical Distribution*

This species is known only from a small area in the eastern part of the Transvolcanic Sierra of central Mexico (Fig. 62).

### *Chorological Affinities*

The range of *O. pseudangustata* is overlapped by that of *O. angustata*, and probably by that of wide-ranging species in the *O. famini* and *O. fulgens* species groups, and *O. batesi* in the *O. aeneipennis* group. It is allopatric in relation to the range of its closest relative, *O. striblingi*, n. sp.

### *Phylogenetic Relationships*

This species is the postulated adelphotaxon of *O. striblingi*, n. sp.

### *Material Examined*

We have seen the type series of *O. pseudangustata* only; for details see above.

### *Onypterygia striblingi*, new species (Fig. 54B, C; 62)

#### *Type Material*

Four specimens, as follows. Holotype male, labelled: "MEX.OAXACA/Vista Hermosa/04 Jul 1982/M. A. Ivie colr." (CUIC). Allotype female, labelled same as holotype (CUIC). Paratypes, two males, one labelled same as holotype; one labelled "MEXICO: Oaxaca/Vista Hermosa/beating, 3-VII-1982/J. B. Stribling, colr." (CUIC).

#### *Type Locality*

Vista Hermosa, Oaxaca is 4.8 km south of Valle Nacional, on Highway 175 (ca. 17°45'N, 96°21'W), at an altitude of 610 m. This locality is near the type locality of *O. exeueros*, n. sp.

#### *Specific Epithet*

This is based on the Latinized genitive form of the surname of J. B. Stribling, one of the collectors of the type series, and a specialist on Ptilodactylidae and related byrrhoid families.

#### *Diagnostic Combination*

With character states of the *O. angustata* species group, restricted as follows. Recognized easily by the pronotum with a single pair of lateral setae, and acuminate elytral apices. The latter feature is similar to that of *O. kathleenae*, n. sp., and *O. longispinis* Bates. However, these species are distinguished readily by the features noted in the key.

#### *Description*

With diagnostic combination of *O. striblingi* and the following.

*Measurements and Proportions of Holotype.*—TL small (8.32 mm), WP/WH intermediate (1.38), LP/WP low (0.86), WP/WPb intermediate (1.12), LE/WE intermediate (1.67).

**Color.**—Antennae with basal and apical antennomeres piceous to black. Palpi piceous. Elytra bright coppery. Femora, tibiae, and tarsi piceous to black.

**Prothorax.**—Pronotum (Fig. 54B). Posterolateral impressions densely punctate; angles obtuse.

**Pterothorax.**—Mesepisternum partially punctate.

**Elytra.**—(Fig. 54C) Elytron, lateral margin slightly sinuate medially. Apex spinose, shorter; sutural apex rounded. Interneurs 2–6 punctate for part of length. Discal setigerous punctures foveate.

**Legs.**—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

**Male Genitalia.**—Internal sac with two spinose sclerites, both on right side, one basal and one nearly at apex.

### Habitat

On vegetation, probably in low montane rain forest.

### Geographical Distribution

This species is known from the type locality only (Fig. 62).

### Chorological Affinities

This species is isolated geographically from the ranges of the other species of the *angustata* group. However, its range is overlapped by the ranges of the *famini*, *aeneipennis*, *pusilla*, and *fulgens* species groups.

### Phylogenetic Relationships

This species is the postulated adelphotaxon of *O. pseudangustata*, based on general similarity and the shared position of the spinose sclerites of the internal sac of the male genitalia.

### Material Examined

We have seen the type series of *O. striblingi* only; for details see above.

## The *fulgens* Species Group

### Recognition

Because of marked interspecific variation, this group is not characterized simply. Included are all species exhibiting a combination of pronotum with lateral margins not or only slightly sinuate posteriorly, and each elytron with a distinct preapical lateral callus, and/or interneur 1 deeper preapically than interneur 2. Further, this group contains all members of the genus with elytra bicolored transversely or with alternating stripes, those with sharply bidentate elytral apices, or combination of fewer than two pairs of lateral pronotal setae and indistinct posterolateral angles.

### Description

With character states of *Onypterygia*, restricted as follows. Body small to large in size, elytra elongate, measurements and proportions as in Table 2.

**Color.**—Ventral surface of body and appendages (except elytra) black to piceous; dorsal surfaces of head, pronotum, and elytra variously black to piceous, aeneous, green, cupreous, or maroon, or various combinations of these, including alternate striping of elytra with cupreous and green, or fasciae of maroon and dark blue.

**Microsculpture.**—Head smooth, without microlines, or microlines distinct, mesh pattern isodiametric. Pronotum smooth, without microlines, or microlines distinct, mesh pattern transverse. Elytra with surface smooth, without microlines, or microlines distinct, mesh pattern isodiametric to transverse, sculpticells flat to slightly convex.

**Luster.**—Dorsal surface shining, or at least elytra dull.

**Chaetotaxy.**—Pronotum without lateral setae, or with one or two pairs. Elytra, in or near interval 3, with two pairs of discal setae to plurisetose. Abdominal sterna IV–VI each with one or more pairs of ambulatory setae, sternum VII of males with one or two pairs of posterior marginal setae, females with two or more pairs.

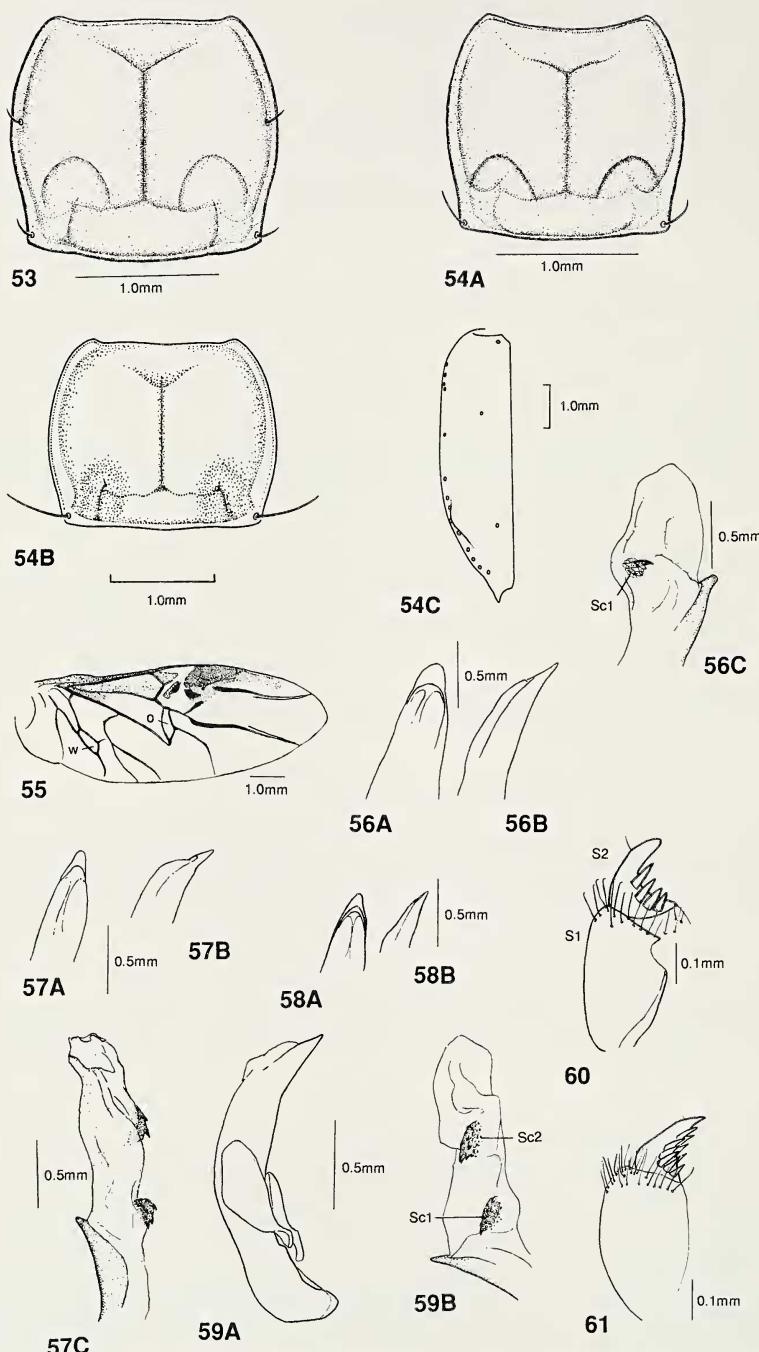


Fig. 53–61.—Line drawings of adult structural features of the *O. angustata* species group. Fig. 53–54A, B, pronotum, dorsal aspect of: 53, *O. angustata* Chevrolat; 54A, *O. pseudangustata*, n. sp.; 54B, *O. striblingi*, n. sp. Fig. 54C, left elytron, dorsal aspect of *O. striblingi*, n. sp. Fig. 55, left hind wing, ventral aspect, of *O. angustata* Chevrolat. Fig. 56–59, male genitalia of: 56, *O. longispinis* Bates: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral

**Head.**—Frons and vertex smooth, without supraorbital carina each side.

**Prothorax.**—Pronotum as in Figure 63–74. Surface smooth or shallowly and sparsely punctate posterolaterally; posterolateral angles obtuse or broadly rounded, lateral margins slightly or not sinuate, beaded partially or completely, or not beaded; posterior pair of setigerous punctures on beads, or in contact with lateral margins; lateral grooves moderately to markedly wide, especially posteriorly. Prosternum with intercoxal process rounded apically.

**Pterothorax.**—Metathorax normal, metepisternum distinctly longer than wide, or metathorax short, metepisternum nearly quadrate.

**Elytra.**—Elongate, humeri fully developed, discal and umbilical setigerous punctures foveate or not. Interneurs fine, shallowly impressed to obsolete; interneur 1 posteriorly on apical declivity more deeply impressed than interneur 2. Preapical lateral calli distinct. Apex acuminate or not; sutural apex angulate, acuminate, or rounded (cf. Fig. 7).

**Hind Wings.**—(Fig. 78, 79) Macropterous, membrane hyaline or infuscated, wedge cell short; or brachypterous.

**Legs.**—Tarsomeres 2–4 ventrally with climbing setae markedly dense (Fig. 11F, G:cs). Tarsomere 5 with ventrolateral setae normally developed (Fig. 11G:vs). Tarsal claws with pectinations more extensive (Fig. 11H).

**Male Genitalia.**—Median lobe (Fig. 80–100) with apical portion short (Fig. 81; 83A, B), narrowly triangular, to elongate (Fig. 89A, B), apex narrow or broadly rounded (Fig. 82A). Internal sac moderately to markedly elongate (Fig. 82C; 87; 88; 97A, B; 98–100), armed variously with spinose sclerites or setose spines.

**Ovipositor.**—Stylomere 2 (Fig. 15, 16, 101–106) slightly falcate, of two types: form 2, ensiform setae ca. 12, and concentrated on or near dorsoapical margin; or form 3, ensiform setae more numerous, in form of dense pad on lateral surface.

### Habitat

Most species of this group are confined to tropical montane forests between 500 and 1500 m altitude, but some range to sea level in tropical deciduous forest, and to pine-fir forest at 2500 m altitude.

### Geographical Distribution

The range of this species group extends throughout Middle America from northern Mexico to Panama, and into northern South America (Fig. 107–110).

### Chorological Affinities

See "Chorological Affinities" for *famini* group, above.

### Phylogenetic Relationships

The *fulgens* species group seems to be the most highly evolved in *Onypterygia*. It is postulated to be the adelphotaxon of the *angustata* group, based primarily on shared details of elytral structure.

### Included Species

This group includes the following 14 species: *O. iris* Chaudoir; *O. championi* Bates; *O. donato* Ball and Shpeley; *O. chrysura* Bates; *O. kathleenae*, n. sp.; *O. exuros*, n. sp.; *O. polytreta*, n. sp.; *O. crabilli*, n. sp.; *O. quadrispinosa* Bates;

←

aspect, with internal sac everted. 57, *O. angustata* Chevrolat: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, apical portion, right lateral aspect, with internal sac everted. 58, *O. pseudangustata*, n. sp. (6 mi. e. Teziutlan, Puebla, Mex.): A, B, median lobe, dorsal and left lateral aspects, respectively. 59, *O. pseudangustata*, (Jalapa, Veracruz, Mex.): A, median lobe and parameres, left lateral aspect; B, median lobe, apical portion, right lateral aspect, with internal sac everted. Fig. 60, 61, ovipositor, left stylomeres 1 and 2, of: 60, *O. angustata* Chevrolat; 61, *O. pseudangustata*. Legend: o—oblongum cell; S1, S2—stylomeres 1 and 2, respectively; Sc1, Sc2—spinose sclerites 1 and 2, respectively; w—wedge cell.

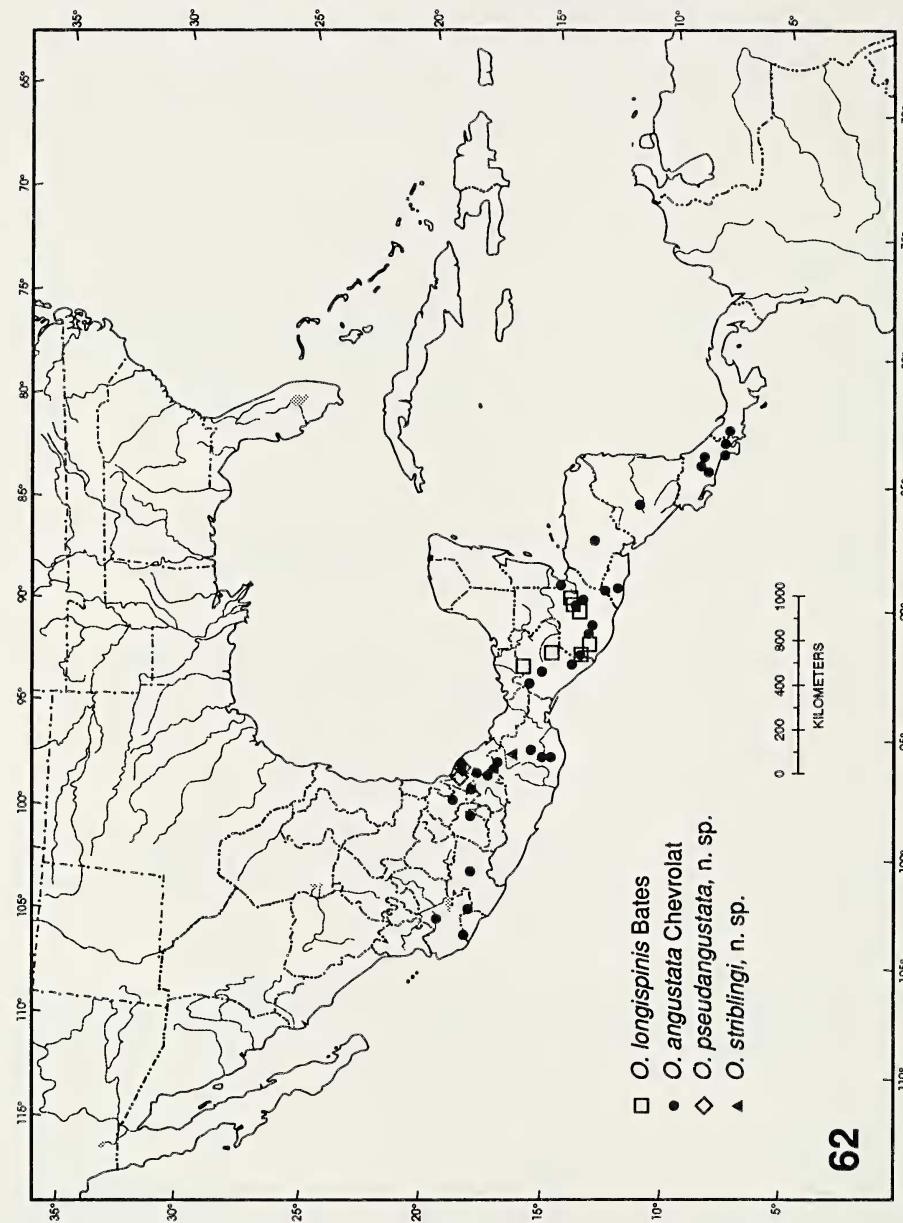


Fig. 62.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the *O. angustata* species group.

*O. scintillans*, n. sp.; *O. fulgens* Dejean; *O. tricolor* Dejean; *O. hoepfneri* Dejean; and *O. sallaei* Chaudoir.

*Onypterygia iris* Chaudoir  
(Fig. 63; 75; 80A–C; 101; 107)

*Onypterygia iris* Chaudoir, 1863:225. Lectotype (here designated), male, labelled: "Iris (Sallé)"; "Ex Musaeo A. Sallé 1897"; (Oberthür-Chaudoir Collection, MNHP). Bates, 1882:130.

*Onychopterygia iris*; Gemminger and Harold, 1868:384 (invalid emendation). Chaudoir, 1878:275.

*Type Locality*

Córdoba, Veracruz, Mexico. In the original description, Chaudoir (1863:225) records for this species only a single locality: Córdoba, state of Veracruz.

*Diagnostic Combination*

With character states of the *fulgens* species group, restricted as follows. The most obvious feature of *O. iris* adults is the longitudinally striped elytra, which is shared with adults of *O. championi*, *O. polytreta*, and *O. donato*. The long metepisternum separates *O. iris* from *O. donato* (metepisternum short, brachypterous). The elytra with nonfoveate discal punctures and simple apices distinguish adults of *O. iris* from those of *O. championi* and *O. polytreta*. Form of median lobe, and internal sac of males and stylomere 2 of females are unique within the genus.

*Description*

With diagnostic combination of *O. iris* and following.

*Measurements and Proportions*.—TL large (11.0 mm), WP/WH low (1.38), LP/WP intermediate (0.76), WP/WPb intermediate (1.24), LE/WE intermediate (1.75).

*Color*.—Head piceous-black. Basal antennomeres black, nonmetallic. Elytra with discal pattern bicolored-striped; coppery and green. Femora, tibiae, and tarsi piceous to black.

*Microsculpture, Mesh Pattern*.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, isodiametric.

*Chaeotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, more than two pairs.

*Head*.—Genae smooth, not rugose. Eyes flattened slightly.

*Prothorax*.—Pronotum (Fig. 63). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins sinuate beaded narrowly, bead indistinct anteriorly.

*Pterothorax*.—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra*.—(Fig. 75) Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow, impunctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomere 1 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe in dorsal aspect (Fig. 80A) with apical portion moderately elongate, narrow, twisted; apex in left lateral aspect (Fig. 80B) very narrowly rounded, essentially acute. Internal sac (Fig. 80C), relatively short; basal lobes two; preapical lobes absent; armature absent.

*Ovipositor*.—(Fig. 101) Stylomere 2 form 1, ensiform setae marginal.

*Habitat*

This species lives in wet tropical montane forest, between altitudes of 800 and 1650 m. Some adults were found on the ground, but the species is probably arboreal.

### Geographical Distribution

The known range of this species is confined to Chiapas and central Veracruz, around Jalapa, Orizaba, and Córdoba (Fig. 107). The record from "Guanajuato" is questionable.

### Chorological Affinities

The range of this species is separated from that of its closest relatives, the Panamanian *O. championi* Bates and the Costa Rican *O. donato* Ball and Shpeley, but is overlapped by other species of the *O. fulgens* group, and by various species of most other groups of *Onypterygia*.

### Phylogenetic Relationships

Ball and Shpeley (1992:407) postulated that *O. iris* is the adelphotaxon of *O. donato* + *O. championi*.

### Material Examined

We have seen 25 specimens of *O. iris*, in addition to records cited by Bates (1882), as follows. All specimens are from localities in Mexico.

**Chiapas:** 1 male, Chiapas-Oaxaca border, 21 km W Rizo de Oro, along ridge SE Cerro Baul, 1615 m, cloud forest, IX.6.1972, C. Mollineux (CASC); 1 male, 8.6 km S Rayon, IX.12.1981, Clark & Coe (AUEM).

**Guanajuato:** Guanajuato, E. Duges (Nègre Coll., MNHP; locality requires confirmation).

**Veracruz:** 1 male, 1 female, Actopan, IX.18.1982, H. Brailovsky (CASC); 1 female, Coatepec, VII.25.1955, P. & C. Vaurie (AMNH); Fortín de las Flores (CSIC, FSCA, UASM); 1 specimen, 5.5 km E Huatusco, cloud forest, 1036 m, VI.21.1966, Ball and Whitehead (UASM); 1 male, Hwy. 140, 1 km N. Huatusco, 1200 m, on logs at night, VIII.14.1987, J. K. Liebherr, D. A. Millman (CUIC); 1 male, Jalapa (MCZC); 1 female, Jalapa, Instituto de Ecología, 1300 m, spider midden, XI.21.1994, Purrington & C. Drake (FFPC); 1 female, 3 km S Jalapa, 1350 m, V.25-30.1991, B. Ratcliffe, J. Ashe, M. Jameson (SEMC); 1 specimen, 3.2 km NE Jilotepec, IX.26 (TAMU); 1 male, Las Minas, 1300 m, at light, VIII.18.1987, D. A. Millman (CUIC); Orizaba, "Sierra de Durango" (Nègre Coll., MNHP; locality probably in Veracruz; see Selander and Vaurie, 1962).

### *Onypterygia championi* Bates (Fig. 64, 76, 81, 107)

*Onypterygia championi* Bates, 1882:130. Lectotype male, labelled: "TYPE H. T." [circular, ringed with red]; "V. de Chiriquí/2-3000 ft./Champion"; "B.C.A. Col. I.1/ Onypterygia/ championi/ Bates"; "Onypterygia/ championi/ Bates" [handwritten]; "LECTO-/TYPE" [circular, ringed with purple]; "♂ BMNH/ LECTOTYPE/ det. D. R. Whitehead [red underline] Onypterygia/ championi/ Bates/ det. D. R. Whitehead"; (BMNH).

### Type Material

Although the BMNH has only the single specimen noted above, and although the description records but a single measurement, Bates may have had more than a single specimen when he described *O. championi*. In the USNM, for example, is a single male, labelled "V. de Chiriquí/2-3000 ft/Champion"; H. W. Bates/ Biol. Cent. Amer."; "m.l. & sac/drawn/D. R. Whitehead"; "Onypterygia/ championi/Bates" [handwritten, in Bates' hand]. But it does not have the "B.C.A." label characteristic of Bates' type material. Possibly then, this specimen was seen by Bates subsequent to publication of the species description. Nonetheless, in view of the uncertainty, the type specimen in the BMNH is regarded as a lectotype.

### Type Locality

Volcán de Chiriquí, Chiriquí, Panama.

### Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. *Onypterygia championi* is the only species of *Onypterygia* with a combination of striped elytra, acuminate elytral apices, and foveate punctures in interval 3.

### Description

With diagnostic combination of *O. championi*, and the following.

*Measurements and Proportions*.—TL large (11.3 mm), WP/WH low (1.55), LP/WP low (0.78), WP/WPB intermediate (1.30), LE/WE intermediate (1.75).

*Color*.—Head dark green. Basal antennomeres partially metallic green. Pronotum dark green. Elytra with discal pattern bicolored-striped coppery and green.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

*Head*.—Genae smooth, not rugose. Eyes flattened slightly.

*Prothorax*.—Pronotum (Fig. 64). Anterior bead complete; lateral beads absent for most of length. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate, beaded narrowly.

*Pterothorax*.—Mesepisternum impunctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron (Fig. 76), humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, shorter; sutural apex rounded. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—(Fig. 81) Median lobe in left lateral aspect with apical portion short, triangular in outline, apex acute. Internal sac moderately elongate; basal lobes and preapical lobes absent; armature two mediopreapical spinose sclerites, left laterally.

*Ovipositor*.—Stylomere 2 form 2.

### Habitat

Specimens of *O. championi* have been collected in wet montane tropical forest.

### Geographical Distribution

This species is known only from the mountains of Costa Rica and Panama (Fig. 107).

### Chorological Affinities

This species is allopatric in relation to the range of its postulated adelphotaxon, the Costa Rican *O. donato*. The range of *O. championi* is overlapped only by the ranges of *O. angustata* (*angustata* group) and *O. tricolor* (*fulgens* group).

### Phylogenetic Relationships

See this topic for *O. iris*, above.

### Material Examined

In addition to the holotype and the male referred to above, we have seen ten specimens of *O. championi* from the following localities.

**COSTA RICA. Puntarenas:** Parque Nacional Amistad, Finca Cafrosa, Est. Mellizas, 1300 m, V.1990, L-S 316100-596100, M. Ramirez & G. Mora (INBC) 1 male, INBIO CR 1000-264710, 1 male, INBIO CR 1000-264711; 3 males, 316100, 599200; same locality, except VI.19–VII.26, 1990, R. Delgado (INBC) 1 male, INBIO CR 1000-667789; 1 male, Est. Biol. Las Alturas, 1500 m, III.23–V.2.1992, L-S-322500, 591300, Coto Brus, F. Araya (INBC). **PANAMA. Chiriquí:** 1 female, Las Lagunas, V.13.1981, J. E. Wappes (JEWC); 1 male, 15 km E Río Sereno, V.23–25.1982, E. Giesbert (CASC); 1 female, 2 km N. Sta. Clara, Hartmann's Finca, 8°51'N, 82°36'W, 1300 m, V.24–25.1977, H. & A. Howden (UASM); 1 male, 1 female, same locality, 1450 m, wet montane tropical forest, VI.15.1995, R. S. Anderson (CMNC); 1 male, 1 female, N. Santa Clara, 8°51'N, 82°46'W, v.31.1977, H. P. Stockwell (UASM).

*Onypterygia donato* Ball and Shpeley  
(Fig. 107)

*Onypterygia donato* Ball and Shpeley, 1992:403. Holotype female (for details of labelling, see original description).

*Type Locality*

La Amistad National Park, Puntarenas, Costa Rica.

*Diagnostic Combination*

With character states of *O. fulgens* species group, restricted as follows. Features are the same as for *O. championi* Bates (see above) plus a reduced metathorax (metepisternum relatively short).

*Description*

With diagnostic combination of *O. donato* and the following.

*Habitus*.—As in Ball and Shpeley, 1992:405, fig. 1.

*Measurements and Proportions of Holotype*.—TL small (8.1 mm), WP/WH low (1.67), LP/WP low (0.80), WP/WPb intermediate (1.20), LE/WE intermediate (1.50).

*Color*.—Head and pronotum dark green. Basal antennomeres black, nonmetallic. Elytra with discal pattern bicolored-striped coppery and green.

*Microsculpture, Mesh Pattern*.—Head, isodiametric; pronotum, transverse; elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae two; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

*Head*.—Genae smooth, not rugose. Eyes flattened slightly.

*Prothorax*.—Pronotum with anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate, beaded.

*Pterothorax*.—Mesepisternum impunctate. Metepisternum shortened slightly, lateral margin slightly longer than anterior margin.

*Elytra*.—Surface smooth. Elytron, humerus obliquely narrowed; elytron, lateral margin narrowly rounded. Apex spinose, shorter; sutural apex angulate. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Brachypterous.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Ovipositor*.—(Ball and Shpeley, 1992:406, fig. 2a–f) Styломere 2 form 1, ensiform setae marginal.

*Habitat*

Probably understory vegetation in dry primary evergreen montane forest (Ball and Shpeley, 1992:407).

*Chorological Affinities*

The ranges of *O. donato* and its close relatives (*O. championi* and *O. iris*) are nonoverlapping. The range of *O. donato* probably is overlapped by the ranges of six other species of *Onypterygia* (Ball and Shpeley, 1992:407).

*Phylogenetic Relationships*

See this topic for *O. iris* above.

*Material Examined*

We have seen the holotype of *O. donato* only.

*Onypterygia chrysura* Bates  
(Fig. 65, 82A–C, 107)

*Onypterygia chrysura*, Bates 1882:131. Lectotype (here designated) female, labelled: “TYPE/ H. T.”

[circular, ringed with red]; S. Gerônimo,/ Guatemala/ Champion”; “B.C.A. Col. I.1/ Onypterygia/ chrysura/ Bates”; “Onypterygia/ chrysura/ Bates” [handwritten, in Bates’ hand]; “LECTO- TYPE” [circular, ringed with purple]; “♀ BMNH/LECTOTYPE/det. D. R. Whitehead [red un-

derline]/ *Onypterygia chrysura*/ Bates/ det. D. R. Whitehead" (BMNH). Paralectotypes (here designated), three additional specimens, similarly labelled (BMNH).

#### Type Locality

San Geronimo, Baja Verapaz, Guatemala (here restricted).

#### Diagnostic Combination

With character states of the *O. fulgens* group, restricted as follows. Pronotum with two pairs of lateral marginal setae; lateral margins wide, not beaded, hind angles obtuse but evident. Elytra metallic green, not vittate, with or without cupreous reflection laterally; interval 3 with three nonfoveate setigerous punctures, apex obtusely angulate, sutural interval angulate but not distinctly denticulate. Sternum VII of female with two pairs of posterior marginal setae. Internal sac of male genitalia long, with long row of setae, without spinose sclerites.

#### Description

With diagnostic combination of *O. chrysura* and the following.

*Measurements and Proportions*.—TL large (11.2 mm), WP/WH intermediate (1.30), LP/WP intermediate (0.90), WP/WPb intermediate (1.20), LE/WE intermediate (1.70).

*Color*.—Head dark green. Antennae with basal articles partially metallic. Pronotum dark green. Elytra with disc concolorous, bright green. Femora metallic, partially black.

*Microsculpture, Mesh Pattern*.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur with setae, or without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

*Head*.—Genae smooth, not rugose. Eyes moderately prominent, convexity average.

*Prothorax*.—Pronotum (Fig. 65). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax*.—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin narrowly rounded. Apex angulate; sutural apex angulate. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures not foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe, in dorsal aspect (Fig. 82A) with apical portion short, apex broadly rounded, lobate; in left lateral aspect (Fig. 82B), apical portion narrow, apex acute. Internal sac (Fig. 82C) markedly elongate; basal and preapical lobes absent; armature, setose spines on ventral surface.

*Ovipositor*.—Stylomere 2 form 2.

#### Variation

Throughout the range of this species, the number of dorsoapical setae of the hind femur varies from 0 to 3. The Costa Rican specimens are distinctive in that the cupreous reflection of the elytra is absent or slight, the interneurs are more distinctly punctulate, and the apex of the median lobe is slightly less lobate. Two females, one collected near Danlí, and the other in Parque Nacional La Muralla, Honduras, are duller green overall, and with the microlines of the elytra more distinct than normal for the species.

#### Habitat

*Onypterygia chrysura* probably lives in wet montane tropical forest, at middle altitudes.

#### Geographical Distribution

This species is known from localities in southern Mexico, Guatemala, Honduras, and Costa Rica (Fig. 107). The absence of specimens from El Salvador and Nicaragua probably reflects lack of collecting in these countries.

### *Chorological Affinities*

The range of *O. chrysura* is overlapped by the ranges of most species of the *O. famini*, *pusilla*, *angustata*, and *fulgens* species groups.

### *Material Examined*

We have seen 17 specimens of *O. chrysura* from the following localities.

**MEXICO.** Chiapas: Ciudad Cuauhtémoc (UASM). COSTA RICA. Puntarenas: Monteverde—1 male, VI.4–6.1980, J. E. Wappes (JEWC); 1 female, V.28–31.1979, J. M. & B. A. Campbell (CNCI); 1 male, 1400 m, V.10.1989, J. Ashe, R. Brooks, R. Leschen (SEMC); 1 male, same, V.23.1989 (SEMC); 1 male, same, H. & A. Howden (UASM); 1 female, San Luis, R. B. Monteverde, VIII.1992, L-N-250850, 449250, Z. Fuentes (INBC); 1 female, 2 km S Santa Elena, 1300 m, VI.2.1979, H. & A. Howden (UASM). San José: 1 female, San José, VI.27.1925, Schmidt (CMNH). GUATEMALA. Baja Verapaz: San Geronimo (BMNH). Escuintla: Zapote (BMNH). Quetzaltenango: Cerro Zunil (BMNH). HONDURAS. Olancho: Parque Nacional La Muralla, MV + UV light, V.24.1995, R. H. Turnbow (RHTC). Paraíso: 1 male, 35 km E Danlí, 700 m, U-V light VI.10.1994, H. & A. Howden (UASM).

### *Onypterygia kathleenae*, new species

(Fig. 11A, B; 66; 83A, B; 102; 107)

#### *Type Material*

Six specimens, labelled as follows. Holotype male, "MEX. Oaxaca 16.9/mi.s. Valle/Nacional 3600'/VIII.14–15.65"; "George E. Ball/D. R. Whitehead/collectors" (USNM). Allotype female: "MEXICO Oaxaca/16.9 mi. s. Valle/Nacional, 3600'/V.4–5.1966"; "George E. Ball/D. R. Whitehead/collectors" (USNM). Four paratypes. Female, labelled same as allotype (UASM). Female, "MEXICO/Oaxaca/Km 87/Tuxtepec/Oaxaca/28-V-87/F Arias" (UNAM). Male, "MEXICO: Chiapas Mu-/nicipio de Angel Al-/bino Corzo (Jalte-/nango), above Finca/Cus-tepec,/1371 m 11.VIII.1981/D. E. & P. M. Breedlove"; "♂ gen. drawn/D. Hollingdale/1991" (CASC). Female, "MEXICO: Chiapas, Mu-/nicipio de Angel Al-/bino Corzo (Jalte-/nango) montane rain/forest above Finca/Cuspec, 1371 m 24.VI.1981/D. E. & P. M. Breedlove"; "PN drawn/D. Hollingdale/1991 (CASC). Female, "GUAT. Zacapa Sierra/de las Minas, 20.3/km w. Teculutan, 21.8/km n. trop. mont. for/1800–1900 m beating/veg. 91-34 8.VI.1991"; "H. F. Howden GUATEMALA EXPED. 1991"; "G. E. and K. E. Ball/D. Shpeley/collectors" (UASM).

#### *Type Locality*

27.2 km south of Valle Nacional, Oaxaca, Mexico.

#### *Specific Epithet*

This species is named in honor of Kathleen E. Ball, collector of one of the paratypes, in recognition of her numerous contributions to elucidating the carabid fauna of Mexico.

#### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. Dorsal surface metallic green. Pronotum with two pairs of lateral marginal setae, posterolateral angles rounded, lateral margins beaded narrowly. Elytra (Fig. 11A, B) acuminate, each with long apical spine. Adults of this species resemble those of *O. exeueros*. For details see "Diagnostic Combination" for that species, below.

#### *Description*

With diagnostic combination of *O. kathleenae* and the following.

*Measurements and Proportions of Holotype*.—TL intermediate (10.5 mm), WP/WH high (1.26), LP/WP intermediate (1.12), WP/WPb high (1.47), LE/WE high (2.05).

*Color*.—Head dark green. Antennae with antennomere 1 bicolored; apical antennomeres rufous.

Palpi rufopiceous. Pronotum dark green. Elytra with disc concolorous, bright green. Femora bicolored, black and rufous; tibiae and tarsi rufous.

*Microsculpture, Mesh Pattern*.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, transverse.

*Chaetotaxy*.—Pronotum, lateral setae two pairs; elytron, discal setae two; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

*Head*.—Genae smooth, not rugose. Eyes flattened slightly.

*Prothorax*.—Pronotum (Fig. 66). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

*Pterothorax*.—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron (Fig. 11A, B), humerus broadly rounded; elytron, lateral margin narrowly rounded. Apex acuminate, spine longer than average (cf. Fig. 11A); sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–2 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe longer than basal portion.

*Male Genitalia*.—Median lobe in dorsal aspect (Fig. 83A) with apical portion very short; apex narrowly rounded; in left lateral aspect (Fig. 83B) apical portion broader than in *O. exeueros*, apex acute. Internal sac, moderately elongate; basal and preapical lobes absent; armature absent, but surface with numerous enlarged microtrichia.

*Ovipositor*.—(Fig. 102) Styломere 2 form 3.

### Habitat

Specimens were collected in tropical montane rain forest at altitudes of 900 to 1900 m.

### Geographical Distribution

The range of this species extends from Oaxaca, on the Atlantic Versant of Mexico to the highlands of Guatemala (Fig. 107).

### Chorological Affinities

This species is allopatric with reference to its putative adelphotaxon, *O. exeueros*, n. sp., although the Oaxacan localities for the two species are only a few kilometers apart. The range of *O. kathleenae* is overlapped by the ranges of several other species of the *O. fulgens* group, by *O. perissostigma*, and by species of the *famini*, *pusilla*, and *angustata* groups.

### Phylogenetic Relationships

Although adults of this species and *O. exeueros* differ markedly in size, they are allopatric in geographical distribution and are strikingly similar in form of elytral apices, in lacking armature from the internal sac of the male genitalia, and in general habitus. On the basis of these considerations, we postulate that *O. kathleenae* and *O. exeueros* are adelphotaxa.

### Material Examined

We have seen the type series of *O. kathleenae* only; for details see above.

### *Onypterygia exeueros*, new species (Fig. 15, 67, 107)

#### Type Material

Seven specimens, labelled as follows. Holotype male, "MEX: Oaxaca/5 mi. SW Esperanza/4 July 1982/R. S. Miller colr"; "♂ Genitalia dissected/& lost/geb-1991" (CUIC). Allotype female, labelled same as holotype (CUIC). Paratypes, five, three (male and two females) labelled same as holotype (CUIC). Female,

"MEX: OAXACA 5 mi/SW La Esperanza/04 Jul 1982/M. A. Ivie colr" (CUIC). Female, "MEXICO/Oaxaca/Km. 87/Tuxtepec--/Oaxaca/28-v-87/F. Arias" (UNAM).

#### Type Locality

Eight km southwest of Esperanza, Oaxaca, Mexico. This locality is close to the type locality of *O. striblingi*, n. sp.

#### Specific Epithet

A Greek word, *exeuros*, used as a noun in apposition. It means ending in a tail or point, and refers to the acuminate elytral apices characteristic of this species.

#### Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Adults of this species are much like those of *O. kathleenae*, but are substantially larger (length more than 12.5 mm, as opposed to less than 11.0 mm), and lack the anterior pair of pronotal setae. As well, the male genitalia differ: in *O. exeuros*, the median lobe in left lateral aspect is more curved, especially the apical portion. In ventral aspect, the apical portion of the median lobe in *O. exeuros* is narrower than in *O. kathleenae*.

#### Description

With the diagnostic combination of *O. exeuros*, and the following.

*Measurements and Proportions of Holotype*.—TL intermediate (12.1 mm), WP/WH intermediate (1.21), LP/WP intermediate (0.89), WP/WPb intermediate (1.16), LE/WE high (1.95).

*Color*.—Head rufopiceous. Antennae with basal and apical antenniferous piceous-black. Palpi piceous. Pronotum rufopiceous. Elytra with discal pattern concolorous, coppery and green. Femora metallic, partially black; tibiae and tarsi piceous-black.

*Microsculpture, Mesh Pattern*.—Head, isodiametric; pronotum, transverse; elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae one pair, posterior pair absent; elytron, discal setae two or three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

*Head*.—Genae rugose, with fine lines. Eyes flattened slightly.

*Prothorax*.—Pronotum (Fig. 67). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax*.—Mesepisternum impunctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, longer than average (cf. Fig. 11A, B); sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres of middle tarsi not sulcate, surface smooth. Hind tarsomere 1 sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe, apical portion short; apex narrowly rounded. Internal sac, moderately elongate; basal and preapical lobes absent; armature absent, but surface with numerous enlarged microtrichia.

*Ovipositor*.—(Fig. 15) Styломere 2 form 2.

#### Habitat

At the type locality, adults probably were collected from the leaves of planted citrus trees. The citrus grove was in an area that had supported lower montane rain forest.

#### Geographical Distribution

This species is known only from the Atlantic Versant of Oaxaca (Fig. 107), at an altitude of about 610 m.

### *Chorological Affinities*

As noted above, this species and *O. kathleenae* are allopatric with respect to one another, although their ranges are nearly in contact. Other species near to or overlapping with *O. exeueros* are *O. angustata*, *O. pseudangustata*, *O. striblingi*, *O. pusilla*, and *O. tricolor*.

### *Phylogenetic Relationships*

This species is the putative adelphotaxon of *O. kathleenae*. For details see "Phylogenetic Relationships" for the latter species, above.

### *Material Examined*

We have seen the type series only; for details see above.

### *Onypterygia polytreta*, new species (Fig. 4A–C; 20; 77; 84A, B; 87; 103; 107)

#### *Type Material*

Eight specimens, labelled as follows. Holotype male: "PANAMA Chiriquí/Pr. Cerro Pando/1535 m./24 May 1973/1535 M. G. Ekis" [handwritten]; "♂ + winged"; "ADP/27606"; "♂ gen. drawn/D. Hollingdale/1991" (USNM). Allotype female: labelled same as holotype, except "♀ + winged"; "ADP/27608" (USNM). Six paratypes. Male, labelled same as holotype, except: "ADP/27607" (USNM). Male, labelled same as holotype, except locality label printed, and: "ADP/27605" (USNM). Male and three females, "V. de Chiriquí/M. de Mathan/1901; [male, labelled: "m. l. and sac/drawn/D. R. Whitehead"] (MNHP).

#### *Type Locality*

Cerro Pando, Chiriquí Province, Panama. This mountain, which attains an altitude of 2441 m, is at 80°55'N, 82°34'W, 18 km northwest of Hato del Volcán (Howden and Young, 1981:6).

#### *Specific Epithet*

From Greek, *polytretos*, meaning full of holes, in reference to the deeply foveate elytra of adults of this species.

#### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. Adults of *O. polytreta* differ from all other *Onypterygia*, except *O. crabilli*, n. sp., by having deep foveae on intervals 3, 5, and 7, and from most others except *O. hoepfneri* by additional setae on abdominal sterna IV–VI. The peculiar elytral color pattern resembles that of *O. iris* and *O. championi*, but *O. polytreta* differs in lack of anterolateral setae and males differ strikingly in details of the genitalia. For differences from *O. crabilli*, see discussion of the diagnostic combination of that species.

#### *Description*

With diagnostic combination of *O. polytreta* and the following.

*Habitus*.—As in Figure 20.

*Measurements and Proportions of Male Paratype*.—TL large (14.8 mm), WP/WH high (1.30), LP/WP intermediate (1.38), WP/WPb low (1.18), LE/WE intermediate (1.84).

*Color*.—Head bright green. Antennae with basal and apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc bicolored-striped, coppery green. Femora, tibiae, and tarsi piceous to black.

*Microsculpture, Mesh Pattern*.—Head, isodiametric; pronotum, transverse; elytra (Fig. 4A), slightly transverse.

*Chaetotaxy*.—Pronotum, lateral setae one pair, anterolateral pair absent; elytron discal setae more

than three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI more than one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

*Head*.—Genae smooth, not rugose. Eyes prominent, convexity marked.

*Prothorax*.—Pronotum (Fig. 77). Anterior bead complete; lateral beads absent. Posterolateral im-pressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax*.—Mesepisternum impunctate. Metepisternum elongate.

*Elytra*.—Surface with prominent discal foveae (Fig. 4B, C), uneven. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, spine shorter; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–3 of middle and hind tarsi not sulcate, surface smooth. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe in dorsal aspect (Fig. 84A), with apical portion short; apex moderately broadly rounded; in left lateral aspect (Fig. 84B), apical portion narrow, dorsal surface curved, apex acute. Internal sac (Fig. 87), markedly elongate; basal and preapical lobes absent; armature with seven spinose sclerites, as follows—two basal (one ventral, one medial), three median (one left lateral, one right lateral, and one ventral), and two apical (one dorsal and one ventral).

*Ovipositor*.—(Fig. 103) Stylomere 2 form 3.

### Geographical Distribution

This species is known only from Chiriquí Province, Panama (Fig. 107).

### Chorological Affinities

This species is allopatric in relation to its postulated adelphotaxon, *O. crabilli*, which is known from Costa Rica. The range of *O. polytreta* is overlapped only by the ranges of *O. angustata*, *O. championi*, and *O. tricolor*.

### Phylogenetic Relationships

Based on similarities in details of the elytra, in armature of the internal sac of the male genitalia, and on proximity but nonoverlapping of geographical ranges, this species and *O. crabilli* are postulated to be adelphotaxa.

### Material Examined

We have seen the type specimens of *O. polytreta* only; for details see above.

### *Onypterygia crabilli*, new species (Fig. 5A–C; 68; 85A, B; 88; 107)

#### Type Material

Seven specimens, labelled as follows. Holotype male, "COSTA RICA, PUNTARENAS/ MONTEVERDE/ May 23–27 1987/ E. GIESBERT, COLL" [hand-written] (FSCA). Allotype female, "C. R. Pnt. 1500 m/Reserva de/Monteverde/ 1–4.VI.1979/J M & B A Campbell" (CNCI). Paratypes, five, as follows. Female, "COSTA RICA: Provin-/cia de Puntarenas, Monteverde Biological/Reserve, at light/15.IX.1990 Norman D. Penny/Cal. Acad. Sc. Coll" (CASC). Female, "Ref. Nac. Fauna Silv./ Tapanti 1150 m Prov./ Cart. COSTA RICA, G./ Mora, F. Quesada, Ene/ 1992, L-N-194000, 559800" (INBC). Female, "Est. Zurqui 500 m antes/ de Tunzel, 1600 m. Prov./ S Jose, COSTA RICA,/ G. Maass. Abr 1991/ L-N-226800, 535200" (INBC). Female, same as previous label, except date: "26 set–oct 1990" (INBC). Male, "Palma, C. R./Aug. 1924"; "Nevermann/Collection/1940" [green paper]; "ADP 57251" (USNM).

#### Type Locality

Monteverde, Puntarenas Province, Costa Rica.

### *Specific Epithet*

This species is named in honor and in memory of our long-time friend and colleague, the late Ralph E. Crabbill, Jr., a noted myriapod specialist, who devoted many years to the classification of North American chilopods.

### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. Like adults of *O. polytreta*, specimens of this species have deep foveae scattered on the disc of the elytra. Unlike *O. polytreta*, however, most of the discal foveae of *O. crabilli* lack setae, and the elytra, rather than green with coppery reflections, are uniformly aeneous, and only females have extra ambulatory setae, and these only on sternum VI. The male genitalia of the two species differ also. See Figures 84A, B; 85A, B; 87; and 88.

### *Description*

With diagnostic combination of *O. crabilli* and the following.

*Measurements and Proportions of Holotype*.—TL intermediate (12.0 mm), WP/WH low (1.22), LP/WP intermediate (0.75), WP/WPb high (1.42), LE/WE intermediate (1.75).

*Color*.—Head bronze-green. Antennae with basal and apical antennomeres rufous. Palpi rufopiceous. Pronotum bronze-green. Elytra with discal pattern concolorous; bronze-green, metallic. Femora rufous; tibiae and tarsi rufous.

*Microsculpture, Mesh Pattern*.—Head, isodiametric; pronotum, transverse; elytra (Fig. 5A), transverse.

*Chaetotaxy*.—Pronotum, lateral setae one pair, posterior pair absent; elytron—discal setae more than three; dorsoapical portion of hind femur without setae; abdominal sterna IV–V with one pair each; sternum VI with two pairs; abdominal sternum VII, marginal setae, male, two or more pairs; female, three or more pairs.

*Head*.—Genae smooth, not rugose. Eyes prominent, convexity marked.

*Prothorax*.—Pronotum (Fig. 68). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax*.—Mesepisternum impunctate. Metepisternum elongate.

*Elytra*.—Surface with prominent discal foveae, uneven. Elytron, humerus broadly rounded; lateral margin broadly rounded. Apex spinose, shorter; sutural apex angulate. Interneurs 2–6 evanescent, completely punctate. Discal and umbilical setigerous punctures (Fig. 5B, C) foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomere 1 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—Median lobe in dorsal aspect (Fig. 85A) with apical portion moderately long; apex narrowly rounded; in left lateral aspect (Fig. 85B), apical portion narrow, curved moderately ventrad, apex acute. Internal sac (Fig. 88), moderately elongate; basal and preapical lobes absent; armature of ten spinose sclerites, as follows—four basal (three left lateral, one dorsal), two median dorsal and two preapical (one dorsal, one ventral), and two apical (one dorsal and one ventral).

*Ovipositor*.—Stylomere 2 form 3.

### *Habitat*

Probably tropical montane forest, at around 1400–1550 m altitude.

### *Geographical Distribution*

This species is known from Costa Rica only (Fig. 107).

### *Chorological Affinities*

This species and its close relative, the Panamanian *O. polytreta*, are allopatric in relation to one another. The range of *O. crabilli* is overlapped by the ranges of *O. angustata*, *O. donato*, *O. chrysura*, *O. quadrispinosa*, *O. scintillans*, and *O. tricolor*. Of these species, *O. donato*, *O. chrysura*, and *O. tricolor* have been collected at or near Monteverde, the type locality of *O. crabilli*.

### *Phylogenetic Relationships*

This species and *O. polytreta* are postulated to be adelphotaxa. For details see "Phylogenetic Relationships" for the latter species.

### *Material Examined*

We have seen the type series of *O. crabilli* only; for details see above.

### *Onypterygia quadrispinosa* Bates (Fig. 69; 70; 86A, B; 107)

*Onypterygia quadrispinosa* Bates, 1882:130. Type material, four specimens, as follows. Lectotype (here designated) female, labelled: "TYPE H. T." [circular label ringed with red]; "LECTO-/ TYPE" [circular label ringed with purple]; "Cerro Zunil/ 4–5000 ft./ Champion"; "B.C.A. Col.I.1/ Onypterygia/ quadrispinosa,/ Bates"; "Onypterygia/ 4 spinosa/Bates" [handwritten]; "♀ BMNH/ LECTOTYPE/ [red underline]/ det. D. R. Whitehead/ Onypterygia.quadrispinosa/ Bates/ det. D. R. Whitehead" (BMNH). Paralectotypes, two males, one female, with same locality and determination labels as lectotype.

### *Type Locality*

Cerro Zunil, Department of Quetzaltenango, Guatemala.

### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. *Onypterygia quadrispinosa* is the only species with coppery-green elytra having sutural denticulae as well as denticulate apices; the denticulae are produced as short spines. In this respect, *O. quadrispinosa* is similar to *O. fulgens*, but the apex of the latter is as a whole less produced, less markedly sinuate subapically, and the elytra are predominantly metallic green or blue.

Despite Bates's (1882:130) observations, the elytra are not markedly striped. From above, they appear mainly maroon, with sutural intervals, margins, and preapical calli metallic green; from behind, the color is mainly metallic green, with a maroon band across the preapical calli.

### *Description*

With diagnostic combination of *O. quadrispinosa*, and the following.

*Measurements and Proportions of Male Paralectotype*.—TL large (14.2 mm), WP/WH low (1.26), LP/WP intermediate (0.83), WP/WPb intermediate (1.22), LE/WE high (2.02).

*Color*.—Head coppery green. Antennae with basal and apical antenniferous piceous to black. Palpi piceous. Pronotum coppery green. Elytra with disc concolorous, coppery green. Femora, tibiae, and tarsi piceous to black.

*Microsculpture, Mesh Pattern*.—Head, microlines partially effaced, isodiametric; pronotum, micro-lines effaced, surface smooth; elytra, transverse.

*Chaetotaxy*.—Pronotum, lateral setae one pair, posterior pair absent; elytron—discal setae two or three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

*Head*.—Genae smooth, not rugose. Eyes prominent, convexity marked.

*Prothorax*.—Pronotum (Fig. 69, 70). Anterior bead incomplete; lateral beads present. Posterior lateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax*.—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex denticulate; sutural apex denticulate. Interneurs 2–6 discontinuous, series of small punctures, impunctate. Discal and umbilical setigerous punctures foveate.

*Hind Wings*.—Macropterous. Wedge cell elongate.

*Legs*.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia*.—(Fig. 86A, B) Median lobe in dorsal aspect (Fig. 86A) with apical portion short, apex narrowly rounded. Internal sac, markedly elongate; basal and preapical lobes absent; armature absent.

*Ovipositor*.—Stylomere 2 form 3.

#### Habitat

Probably this species inhabits montane tropical forest.

#### Geographical Distribution

This species is known from two widely separated areas: the Pacific Versant of Guatemala, and the Atlantic and Pacific versants of Costa Rica (Fig. 107).

#### Chorological Affinities

The range of *O. quadrispinosa* is overlapped by the ranges of many species of *Onypterygia*, included in the *famini*, *pusilla*, *angustata*, and *fulgens* species groups. Other species collected on Cerro Zunil, and possibly syntopic there with *O. quadrispinosa* are *O. chrysura* and *O. longispinis*. Geographical relations between *O. quadrispinosa* and its putative adelphotaxon, *O. scintillans*, n. sp., cannot be specified, because the location of the latter is not known.

#### Phylogenetic Relationships

The putative adelphotaxon of *O. quadrispinosa* is *O. scintillans*, n. sp., based on shared character states of angulate or acuminate sutural apices, and long internal sac of the male genitalia that is without spinose sclerites or with only one.

#### Material Examined

In addition to the type series, we have seen three specimens of *O. quadrispinosa*, all from Costa Rica, as follows.

**Alajuela:** 1 female, R. San Lorencito, R. F. San Ramon, 5 km N Colonia Palmarena, 900 m, L-N-244500, 470700, VI.13–18.1993 (INBC). **Cartago:** 1 female, La Suiza de Turrialba, 1923, Pablo Schild (CMNH). **Puntarenas:** Alajuela, Peñas Blancas XII.1–12.1986, E. Cruz (UASM).

### *Onypterygia scintillans*, new species (Fig. 89A, B; 107)

#### Type Material

One specimen only. Holotype male, labelled: “Holo-type” [circular label, ringed with red]; “Col. Zeledón/ [illegible writing]/X11.25”; “Nevermann/Collection/1940” [green paper]; “PN ♂ gen/drawn/D. Hollingdale/1990” (USNM).

#### Type Locality

The labelling is inadequate to establish the place of the type locality. Since the specimen was in the Nevermann collection, we assume that it was taken in Costa Rica. We have been unable to locate a gazetteer or map reference to “Col. [= Colonia?] Zeledón.”

#### Specific Epithet

A Latin present participle, *scintillans*, of the verb *scintillare*, meaning to sparkle; in allusion to the gleaming dorsal surface of the holotype.

#### Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Similar to *O. quadrispinosa* in size and most other features, the holotype of *O. scintillans* has its elytral apices rounded rather than angulate.

#### Description

With diagnostic combination of *O. scintillans* and the following.

*Measurements and Proportions of Holotype*.—TL moderate (13.0 mm), WP/WH low (1.33), LP/WP intermediate (0.74), WP/WPb intermediate (1.31), LE/WE high (1.87).

*Color*.—Head dark green. Antennae with basal and apical antennomeres rufous. Palpi piceous. Pronotum dark green. Elytra with disc concolorous, dull green. Femora, tibiae, and tarsi rufous.

*Microsculpture, Mesh Pattern.*—Head, isodiametric; pronotum, microlines effaced, surface smooth; elytra, isodiametric.

*Chaetotaxy.*—Pronotum, lateral setae one pair, anterior pair absent; elytron—discal setae two; dorsopapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII with two pairs of marginal setae.

*Head.*—Genae smooth, not rugose. Eyes prominent, convexity marked.

*Prothorax.*—Pronotum. Anterior bead incomplete; lateral beads present, posteriorly only. Postero-lateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

*Pterothorax.*—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra.*—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex rounded; sutural apex angulate. Interneurs 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures foveate.

*Hind Wings.*—Macropterous.

*Legs.*—Tarsomeres of middle and hind tarsi not sulcate, surface smooth. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

*Male Genitalia.*—Median lobe in dorsal aspect (Fig. 89A) with apical portion moderately long, apex narrowly rounded; in left lateral aspect (Fig. 89B), apical portion slender, apex acute. Internal sac, markedly elongate; basal and preapical lobes absent; armature one spinose sclerite.

*Ovipositor.*—Unknown.

### *Habitat and Geographical Distribution*

Unknown, other than that the type locality probably is in Costa Rica (Fig. 107).

### *Chorological Affinities*

Unknown.

### *Phylogenetic Relationships*

This species is the putative adelphotaxon of *O. quadrispinosa*. See this topic for the latter species, above.

### *Material Examined*

We have seen the holotype of *O. scintillans* only; for details see above.

### *Onypterygia fulgens* Dejean

(Fig. 11F–H; 71; 90A, B; 91A, B; 92A, B; 97A, B, 104; 108)

*Onypterygia fulgens* Dejean, 1831:348. Lectotype (here designated) female, labelled: “Mexique/ fulgens mihi” [green paper]; “Chevrolat” [green paper]; “Ex Musaeo/Chaudoir” [red print] (MNHP). Castelnau, 1840:42; Bates, 1882:131. Heyne, 1895:25.

*Onychopterygia fulgens*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

*Onypterygia thoreyi* Mannerheim, 1844:869. Lectotype (here designated) male labelled “Acapulco” [script]; “Thoreyi Mannerh.” [script]; “Ex Musaeo/Thorey” (MNHP). Bates, 1882:131. Heyne, 1895: 25. New synonymy.

*Onychopterygia thoreyi*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

### *Type Locality*

For typical *O. fulgens*, the type area is Mexico, with type locality here restricted to Orizaba, Veracruz, Mexico.

The type locality for *O. thoreyi* is Acapulco, Guerrero, Mexico.

### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. Pronotum without marginal setae; also, elytra metallic green or blue, with or without coppery reflections, elytra apically with apex and apex of suture angulate, and sternum VII of females with more than two pairs of posterior marginal setae.

### *Description*

With diagnostic combination of *O. fulgens* and following.

*Measurements and Proportions.*—TL intermediate to large (10.5–16.5 mm), WP/WH low (1.18), LP/WP high (0.84), WP/WPb intermediate (1.26), LE/WE high (1.74).

**Color.**—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous, bright green to dark blue, laterally color of disc or with bright coppery reflections. Femora metallic, partially black; tibiae and tarsi piceous to black.

**Microsculpture, Mesh Pattern.**—Head, isodiametric; pronotum, isodiametric; elytra, isodiametric.

**Chaetotaxy.**—Pronotum, lateral setae absent; elytron—discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

**Head.**—Genae rugose, with fine lines. Eyes prominent, convexity marked.

**Prothorax.**—Pronotum (Fig. 71). Anterior bead incomplete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

**Pterothorax.**—Mesepisternum partially punctate. Metepisternum elongate.

**Elytra.**—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex denticulate; sutural apex denticulate. Interneurs 2–6 continuous, moderately deep, punctate for part of length. Discal and umbilical setigerous punctures not foveate.

**Hind Wings.**—Macropterous.

**Legs.**—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion. Climbing setae (cs), setation of tarsomere 5 (vs), and pectination (p) of claws as in Figure 11F–H.

**Male Genitalia.**—Median lobe in dorsal aspect (Fig. 90A–92A) with apical portion short to very short, apex acute; in left lateral aspect (Fig. 90B–92B), apical portion narrow, more or less parallel sided, apex acute. Internal sac (Fig. 97A, B) markedly elongate, without basal and preapical lobes; armature with about 14 spinose sclerites, as follows—two basal-dorsal (one ventral, one right-lateral), six premedial dorsal, six preapical (three left-lateral and three right-lateral).

**Ovipositor.**—(Fig. 104) Styломere 2 form 3.

### Variation

This species varies notably in color, the junior synonym, *O. thoreyi*, designating a geographically distinctive form of *O. fulgens*. We found no significant variation in either male genitalia or female ovipositor; the number of spinose sclerites on the internal sac varies, but without marked geographical correlation.

All specimens examined from Central America, Chiapas (107) and Oaxaca (9), and nearly all from Veracruz (100) are typical *O. fulgens*: elytra shiny, intervals flat, color bright metallic green with coppery reflections, at least apically; legs uniformly dark. The sole specimen from Minatitlán, Veracruz, is typical “*O. thoreyi*”: elytra comparatively dull, intervals convex, no coppery reflections; legs red. One specimen in a series of otherwise typical *O. fulgens* from 6.2 mi (10 km) NW Jalapa has reddish legs, but normal coppery reflecting elytra.

Six specimens, from San Luis Potosí, match typical *O. fulgens* except that only one has distinctly coppery reflecting elytra; since the elytra of this series tend to be shiny dark blue rather than green, they resemble the blue variety recorded by Chaudoir (1878:275) and Bates (1882:131) from Cuernavaca, Morelos. We found no recent specimens of the noncoppery, shiny, dark blue, black-legged Cuernavaca form of *O. fulgens*, but we have seen old specimens in European collections. Most specimens from Morelos are red-legged, typical “*O. thoreyi*,” except one black-legged *O. fulgens*.

A broad hybrid zone between *O. fulgens* “*thoreyi*” and nominotypical *O. fulgens* is in Guerrero (44 specimens) and Morelos (39 specimens): 12 specimens have coppery reflections as in typical *O. fulgens*, but seven of them are red legged; and 71 have noncoppery elytral reflections, as in *O. fulgens* “*thoreyi*,” but only 58 of them have red legs.

North of the Río Balsas in Guerrero (Apipilulco, Buena de Cuellar, Iguala, and Taxco) and Morelos, 59 specimens have red legs and noncoppery-reflecting elytra (91%), five have black legs and noncoppery-reflecting elytra (7%), and one has red legs and coppery-reflecting elytra (2%). South of the Río Balsas in Guerrero

(Chilpancingo, Mazatlán, and Omiltemi), 21 specimens have noncoppery-reflecting elytra, and 13 of these are red legged (40%) and eight are black legged (25%); and 11 have coppery-reflecting elytra, of which six are red legged (19%) and five are black legged (16%). Chilpancingo is the only sampling area represented both by a definite mix of coppery- and noncoppery-reflecting elytra (ratio about 2:1) and also by numerous specimens that combine coppery-reflecting elytra with pale legs. In the Chilpancingo area, the ratio of red-legged to dark-legged is about 3:2, in contrast to about 9:1 toward Taxco and into Morelos.

Specimens from the following areas are all *O. fulgens "thoreyi,"* with noncoppery-reflecting green or blue elytra: localities north of the Río Grande de Santiago—Chihuahua and Sonora: four specimens, all red legged. Sinaloa: 46 red legged (32%) and 98 black legged (68%). Localities south of the Río Grande de Santiago—Nayarit and northwestern Jalisco (Plan de Barranca and Magdalena), 41 red legged (38%) and 65 black legged (62%); 23 km S Tepic, Nayarit, 30 red legged (50%) and 30 black legged (50%); eastern Jalisco (Ajijic, Guadalajara), near Río Santiago headwaters, 68 red legged (67%) and 34 black legged (33%); and Colima and southwestern Jalisco (Casimiro Castillo, La Huerta, Puerto Vallarta, and Talpa de Allende), 16 red legged (48%) and 17 black legged (52%).

Thus, within *O. fulgens "thoreyi,"* there is a cline in leg color, with red leggedness increasing from about 32% in Sinaloa to about 90% around Cuernavaca, but the red-legged specimens from the Río Mayo in Chihuahua and Sonora may represent a population discontinuous from that in Sinaloa. In the Chilpancingo area of Guerrero, where red-legged *O. fulgens "thoreyi"* meet black-legged nominotypical *O. fulgens*, numerous intermediates occur (Fig. 108, white diamond-shaped marks). In contrast, there is little evidence that *O. fulgens "thoreyi"* readily hybridizes with eastern populations of *O. fulgens*; the similar and apparently scarce blue forms of *O. fulgens* from Morelos and San Luis Potosí might represent such hybridization, but these darkly colored forms are unlike the hybrid forms in Guerrero.

The single specimen of typical *O. fulgens "thoreyi"* from Minatitlán, Veracruz, might be an erroneous record, or it may represent a population of true *O. fulgens "thoreyi"* inside the range of nominotypical *O. fulgens*. There may have been a partial development of reproductive isolation between *O. fulgens "thoreyi"* and nominotypical *O. fulgens* (perhaps represented by character displacement in leg color near the point of contact between them) which broke down subsequently in the south and southwest, but not in the east.

#### Habitat

Adults of *O. fulgens* live on vegetation in forests of various types, ranging in altitude from near sea level to about 2500 m. During the period May through September, many specimens have been taken at night using UV light traps; during the day, they are obtained by sweeping or beating vegetation. From December through May, they are commonly collected from bromeliads. Specimens have been collected on the ground, but in tree-fall litter.

#### Geographical Distribution

The range of this species extends from southern Sonora and Chihuahua in the west to southern San Luis Potosí in the east, southward to Costa Rica, with a population in Venezuela that is perhaps isolated from the Middle American part of the species' range (Fig. 108). Nominotypical *O. fulgens* ranges north to Ve-

racruz and Oaxaca, *O. fulgens* "thoreyi" ranges from Sonora south to Michoacán and Jalisco, and intermediates occur in Guerrero and Morelos.

### *Chorological Affinities*

The range of this species overlaps the ranges of all other species groups of *Onypterygia*, and as well the ranges of the species to which it seems to be most closely related: *O. tricolor*, *O. hoepfneri*, and *O. sallei*.

### *Material Examined*

We have seen 1392 adults of this species, collected in the following localities.

**MEXICO.** **Chiapas:** 11.5 km S Amatenango del Valle (UASM); Chiapa de Corzo (USNM); jct. Hwy. 190 & 195, ne. Chiapa de Corzo (UASM); 1 female, 2 km S Chicoasén, rd. to Mirador, H. F. Howden, VI.18.1989 (UASM); 1 male, Cinco Cerros, Km 30 on Hwy. 190, 1500 m, V.8.1989, H. F. Howden (UASM); 1 male, same, VI.9.1990, H. & A. Howden (UASM); 1 male, El Chorreadero, 8.8 km E Chiapa de Corzo, VI.22.1990, R. H. Turnbow (RHTA); 52.3 km E Comitán, 8 km N. Frontera Comalapa; 1 male, 7 km NE Huixtla, 305 m, X.7.1972 (CASC); 1 specimen, 11 km S Jitotol, bromeliads, V.5.1966, Ball and Whitehead (UASM); 1 female, Km 20, Motozintla–Comitán Hwy., 900 M, VII.8.1988, A. Cadena, L. Cervantes (UNAM); 3 males, Nuevo Amatenango, 1000 m, VII.8.1988, A. Cadena, L. Cervantes (UNAM); 1 female, 9.8 km N. Ocosingo, Chincultic, VI.20.1990, R. H. Turnbow (RHTC); 1 female, Municipio Oxchuc, Rancho San Ramón, VII.12.1975, T. A. Hubbell (U. Ariz. Coll); 14.8–20.1 km N. & 16 km W Ocozocoautla (UASM); Palenque (UASM); 2 males, Parque Nacional El Aguacero, 16 km W Ocozocoautla, V.9.1989, H. F. Howden (UASM); 2 females, same, VI.12.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 1 female, Parque Laguna Belgica, flight intercept trap, 970 m, VI.08.1991, J. S. Ashe (SEMC); Parque Nacional Montebello, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 5 males, 3 females, Parque Nacional Sumidero, 1100 m, V.25.1990, H. F. Howden (UASM); 1 male, same, V.26.1990, B. D. Gill (CMNC); 1 female, same, V.29.1990, H. & A. Howden (UASM); 1 male, 1 female, same, Coyota Mirador, 1700 m, VI.10.1989, H. F. Howden (UASM); 3 males, Parque Nacional Sumidero, VI.1–12.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 1 male, same, 700 m, flight intercept trap, J. S. Ashe (SEMC); 8 specimens, Pueblo Nuevo, 1547 m, bromeliads, V.25.1966, Ball and Whitehead (UASM); 5.0 km S Pueblo Nuevo; 1 specimen, 13 km E Rizo de Oro, Rte. 190 (UASM); 1 male, Ruinas Chincultic, 1500 m, VI.3.1990, H. & A. Howden (CMNC); 2 females, same, rd. to Montebello, VI.12.1989, H. F. Howden (UASM); 13.8 km E, 23.8 km SE, & 43.4 km W San Cristóbal de las Casas (UASM); 1 specimen, E slope Sierra de Colmena, nr. La Caverna, Arroyo Santa María, G. E. Ball, K. E. Ball, and P. Meyer (UASM); 27.4 km SE Teopisca (UASM); 3 males, km 54, Tuxtla Gutiérrez–Villa Flores, 530 m, VII.12.1988, A. Cadena, L. Cervantes (UNAM); 2 males, 45 km E Tuxtla Gutiérrez, 1400 m, V.28.1990, H. & A. Howden (UASM); 1 female, 18 km W Tuxtla Gutiérrez, X.23.1988, R. H. Turnbow (RHTC); 21.6 km W, 17 km W, 32.2 km S Tuxtla Gutiérrez; 1 ex., Yaxoquintela, 16°58'N, 91°47'W, 560 m, VIII.21.1978, J. E. Rawlins (CMNH); same, IX.17.1978. **Chihuahua:** El Limón, Río Mayo; Gusarremos, Río Mayo (CASC). **Colima:** Colima (UASM, USNM); 1 male, 20 km NE Colima, VII.17.1990, J. E. Wappes (JEWC); 20.8 km E Manzanillo (UASM); 1 female, 14 km E Minatitlán, VI.17.1990, J. E. Wappes (JEWC); Mt. Colima; Tecuizitlan. **Distrito Federal:** Mexico (USNM). **Durango:** Ventanas (= Villa Corona; Selander and Vaurie, 1962). **Guerrero:** Apipilulco (USNM); 5.3 km N. rd. to Buenavista de Cuellar; Chilpancingo (FSCA, USNM); 29 km S & 35.4 km N. Chilpancingo (CNCI); 1 male, 1 female, km 95, Coyuca-Zihuatanejo, VII.25.1985, F. Arias, R. Barba (UNAM); 6 specimens, 18 km S El Paraíso, 900 m, VII.5.1982, J. E. Rawlins (CMNH); 12.9 km E Iguala; 1 female, 16 km NW Iguala, 1160 m, IX.12–19.1982, J. A. Chemsak (CISC); Ixcuinatoyac (USNM); 45.1 km S Mazatlán; Omiltemi (UASM); 1 female, Ostotitlán, X.22.1988, H. Brailovsky (UNAM); Rancho Papagaio; 1 specimen, 2.5 km off Rte. 95, road to San Juan Tetelcingo (UASM); Taxco (CNCI); 2 males, 12.9 km N. Taxco, 2000 m, VI.19.1959, H. E. Evans (CUIC); Tepellapa; Tierra Colorada. **Hidalgo:** Ajacuba (CASC). **Jalisco:** 10 males, 7 females, Ajijic (UASM); Ajijic (USNM); 1 male, 6 km S Autlán, VII.16.1990, J. E. Wappes (JEWC); Casimiro Castillo (MCPM); 1 female, 0.8 km N. Ciudad Guzmán, X.6.1966, R. F. Smith (CISC); 1 male, 11.7 km S Cocula (UASM); 1 specimen, 8.8 km NW Cocula (UASM); 1 specimen, 15 km W El Texquequite, 1046 m, VI.30.1977, J. E. Rawlins (CMNH); 8 specimens, Guadalajara (CMNH); 1 female, same, VII.13.1959, H. E. Evans (CUIC); 1 male, Guadalajara, Ameca, VIII.1993 (ACCS); 1 male, 2 females, 6.4 km SW Guadalajara, VI.29.1963, J. Doyen (CISC); 31 km N. Guadalajara; 16.4 km NE La Huerta (UASM); 32.2 km NE Magdalena; 4.8 km SE Plan de Barrancas (UCDC); Puerto Vallarta (CASC); 6 males, 6 females, 33.8 km S Puerto Vallarta, on Hwy. 200, 725 m, U-V light, VII.21.1986, S. M. McCleve, P. Jump (UASM); 6.4 & 10.5 km S Talpa de Allende (UASM); 1 female, Tuxpan, 1650 m, VI.24.1979, M. Zunino (ACCS); 17 males, 6

females, Volcán Tequila, 10–14 km SSW Tequila, 2134 m, X.8.1974, D. E. & J. A. Breedlove (CASC). **México:** 4.8 km S Ixtapan de la Sal (UASM); Temascaltepec, Bejucos, H. E. Hinton (MCZC). **Morelos:** Alpuyeca; 1 male, Cuernavaca, 1524 m, VI.19–29.1959, H. E. Evans (CUIC); 7 km E Cuernavaca (Tejalpa); 14.6 km E Cuernavaca (Cañon de Lobos) (CNCI); 14 specimens, Cañon de Lobos, Km 19, E Cuernavaca, 1120–1375 m, VII.3.1992, C. Bellamy (CMNH); 19.3 km E Cuernavaca; Progreso; Puente de Ixtla; Tequesquitengo (UASM); Xochicalco (UASM); Xochitepec (USNM). **Nayarit:** 3 females, Acaponeta, VII.15.1960, P. H. Arnaud, Jr., E. S. Ross, D. C. Rentz (CASC); Ahuacatlán (UASM); 1 female, vic. Compostela (MCZC); Ixtlán del Río (USNM); La Mesa de Nayar; 3.2 to 14.0 km E San Blas (USNM); San Juan Peyotán; 4 specimens, Tepic, 900 m, VI.27.1977, J. E. Rawlins (CMNH); 60 specimens, 23 km S Tepic, 1077 m, VII.17.1977, J. E. Rawlins (CMNH); 3 males, 30 km SE Tepic, 1270 m, oak-pine forest, U-V light, VII.20–21.1993, S. McCleve, G. E. & K. E. Ball (UASM); 31.1 & 38.6 km se Tepic (UASM). **Oaxaca:** 32.2 km S Juchatengo (UASM); 1 male, Juquila Mixes, dist. de Yautepec, VI.1970, W. S. Miller; 3 males, 3 females, same, VI, VIII & IX.1972; 2 males, 1 female, same, VIII & IX.1974 (CNCI); 2 females, Hwy. 131, 184 km S Oaxaca, V.27–30.1971, D. E. Bright (CNCI); 36 km N. Puerto Escondido (UASM); 4 males, 3 females, San Juan Lachao, Mun. de Juquila, IV.14.1965, G. Halfter (CNCI); San Miguel Panixtlahuaca; Tehuantepec. **Puebla:** 8.0 km S Izúcar de Matamoros (UASM); Putla. **San Luis Potosí:** 39.7 km E Landa de Matamoros (UASM). **Sinaloa:** 1 male, Choix, VII.5.1968, T. A. Sears (UCDC); 12.9 km NE Concordia (CASC); 9.7 km S Culiacán; 4.8 km E Culiacán (MCPM); 12.9 km S Elota (UCDC); 25 km E El Palmito; Mazatlán (MCPM); 4 to 16 km N. Mazatlán (MCPM); 1 female, 8 km N. Mazatlán, VII.30.1964, W. C. McGuffin (CNCI); 2 females, same, VIII.5–7.1964, H. F. Howden (CNCI); 1 female, 48 km N. Mazatlán, Microondas El Indio, 412 m, trop. decid. forest, U-V light, 86–16, VIII.6.1986, Ball, Frania, Mulyk (UASM); Venedillo (CASC); 3 males, 2 females, 43.2 km E Villa Union, VII.26.1964, H. F. Howden (CNCI); 1 male, 2 females, 33.6 km E Villa Union, VII.25.1964, H. F. Howden (CNCI). **Sonora:** Charuco, Río Mayo (CASC). **Veracruz:** Coatepec, III.15.1929 (Fall Coll-MCZC); Córdoba (USNM); 1 specimen, 3.9 km NE Coscomatepec, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); 18 specimens, jct. Rte. 125 and microondas road 7, 7.2 km NE Coscomatepec, 9.7 km N El Encino, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); Fortín de las Flores (UASM); 16.7 km SW Huatusco (UASM); Jalapa (USNM); 4.8 & 10.0 km NW Jalapa (UASM); 1 female, 3 km S Jalapa, V.25–30.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 2 specimens, 35 km. E. Jilotepec, bromeliads, XII.17.1978, G. E. and K. E. Ball (UASM); Lago de Catemaco (UASM); Minatitlán (UASM); 1 ex., Orizaba, VII.27.1960 (MCPM); 8.4 km E Orizaba (UASM); Presidio (USNM); Río Blanco; San Andres Tuxtla (USNM). **COSTA RICA.** 3 specimens, "Costa Rica" (CMNH). **EL SALVADOR.** **La Libertad:** 4 specimens, Boquerón, nr. Santa Tecla (CNCI, UASM). **Santa Ana:** 3 specimens, 6 km W Hiway CA1, above Lago de Coataapeque, 853 m, VI.1 (USNM); Cerro Verde (USNM). **San Salvador:** San Salvador (BMNH). **GUATEMALA.** **Alta Verapaz:** 7 specimens, Panzos (MCZC). **Baja Verapaz:** 2 males, 3 females, 8 km S Purulhá, 1660 m, V.19.1991, R. S. Anderson (CMNC); 21 males, 11 females, 8 km S Purulhá, tropical montane forest, 1660 m, V.19–27.1991, G. E. & K. E. Ball & D. Shpeley (UASM); 1 male, 1 female, same, VI.4.1993, H. & A. Howden (UASM); 1 specimen, 32 km S Rabinal, U-V light (USNM); 3 specimens, San Gerónimo (MCZC). **Chichicastenango:** 1 specimen, El Naranjo (USNM). **Chimaltenango:** 3 specimens, S. P. Yecopapa (FMNH); 1 specimen, Municipio Yecopapa, Finca Recreo (FMNH). **Huehuetenango:** 1 specimen, La Mesilla (USNM). **Izabal:** 1 female, Cerro San Gil, 8 km N. Las Escobas, V.11.1993, H. & A. Howden (UASM). **Zacapa:** 3 males, 3 females, 3.5 km SE La Union, cloud forest, 1500 m, VI.4.1991, R. S. Anderson (CMNC); 3 males, 2 females, same locality, VI.23.1993, R. Brooks, J. S. Ashe, #084 (SEMC); 1 male, 3 km S La Union, 1400 m, VI.15.1994, H. & A. Howden (UASM); 8 males, 5 females, Sierra del Espíritu Santo, 9 km SE La Union, tropical montane forest, U-V light, 1400–1500 m, G. E. & K. E. Ball & D. Shpeley (UASM). **HONDURAS.** **Federico Morazán:** 6 males, 3 females, Cerro Uyuca, 30 km E Tegucigalpa, U-V light, 1800 m, V.19–VI.6, 1994, H. & A. Howden (UASM); 1 specimen, Zamarano, 777–793 m (UMMZ). **Olancho:** 3 males, Parque Nacional La Muralla, MV + UV light, V.24–VI.1.1995, R. H. Turnbow (RHTC). **Paraiso:** 1 female, 19.4 km SE Zamarano and 9.4 km SE Galera, 1460 m, 13°24'N, 86°55'W, "Los Lavaderos", ex treefall litter, VI.11.1994, J. S. Ashe and R. Brooks #075 (SEMC). **NICARAGUA.** **Matagalpa:** Matagalpa (FSCA). **VENEZUELA.** **Aragua:** 2 specimens, Rancho Grande, V.15.1973, G. Ekis (USNM).

*Onypterygia tricolor* Dejean  
(Fig. 72; 78; 93A, B; 94A, B; 98; 105; 109)

*Onypterygia tricolor* Dejean, 1831:349. Lectotype (Here designated), male labelled: "Orizaba" [green paper]; "tricolor Chevr./in Mexico" [green paper]; "Chevrolat" [green paper]; "Ex Musaeo/

Chaudoir" [red print] (MNHP). Chevrolat, 1835:157. Chaudoir, 1837:12. Castelnau, 1840:42. Bates, 1882:131. Heyne and Taschenberg, 1908:25 (see Heyne, 1895). *Onypterygia tricolor*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275. *Onypterygia tricolor v. dimidiata* Chevrolat, 1835:157. Type material: not seen; types not fixed. There may be suitable specimens in OXUM, but validation of this name was unintentional. Synonymized by Csiki, 1931:744. *Onypterygia apicalis* Chaudoir, 1837:12. Lectotype (here designated) male, labelled "var. apicalis Chaud." and "Ex Musaeo Chaudoir" [red print] (MNHP). Bates, 1882:131. *Onypterygia apicalis*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275. New synonymy.

#### *Names and Type Material*

Possible type material of *O. tricolor* seems restricted to three specimens in the Oberthür-Chaudoir collection (MNHP), each with green Dejean labels. Since Dejean indicated in the original description that the specimen was received from Chevrolat, the male specimen labelled "Höpfner" is rejected. Of the other two specimens, one has a determination label, and is selected here as lectotype.

Chevrolat (1835), after a brief Latin description of *O. tricolor*, wrote: "Var. β Viridis, elytris rubris cum tertia parte apicale coeruleo-violaceis. *Callichroa dimidiata*, Hoepfner (inedita)." (This combination of name and author, being unpublished previously, has no status nomenclaturally.) Following a description and discussion of *O. tricolor* in French, he wrote a similar note in French for *Callichroa dimidiata*. These excellent descriptive statements comprise the earliest validation of the name *O. dimidiata*, albeit unintentional. Thus, this name cannot be attributed to Heyne and Taschenberg (1908; see Heyne, 1895), as done by Csiki (1931) and Blackwelder (1944).

The name *O. apicalis* was based on the western color form, with the dark apical coloration reduced in extent. Only one specimen in Chaudoir's material seems eligible as type, but he did not so state in the original description. Thus, the specimen labelled "var. apicalis Chaud" is selected as lectotype. This label implies an afterthought, since originally, Chaudoir described *O. apicalis* as a distinct species. Chaudoir (1878) considered as synonyms the names *O. dimidiata* and *O. apicalis*.

#### *Type Localities*

The type area of nominotypical *O. tricolor* is Mexico, and the type locality is restricted here to Orizaba, Veracruz, Mexico.

The type area of *O. tricolor dimidiata* is "environs de Mexico."

The type area of *O. tricolor apicalis* is Mexico, and the type locality is restricted here to 8.7 km east of Cuernavaca, state of Morelos.

#### *Diagnostic Combination*

With character states of the *O. fulgens* group restricted as follows. Elytra bicolored, banded, rufotestaceous basally, and violaceous black apically. Also, pronotum with a single pair of setae (posterolaterals), elytra posteriorly each bidenticulate, and female sternum VII posteriorly with more than two pairs of marginal setae.

#### *Description*

With diagnostic combination of *O. tricolor* and the following.

*Measurements and Proportions*.—TL intermediate to large (11.5–14.5 mm), WP/WH low (1.32), LP/WP intermediate (0.78), WP/WPb low (1.18), LE/WE high (1.85).

*Color*.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous to black. Palpi piceous. Pronotum bright green. Femora metallic, partially black; tibiae and tarsi piceous-black.

*Microsculpture, Mesh Pattern.*—Head, microlines partially effaced, isodiametric; pronotum, with microlines effaced, surface smooth; elytra, isodiametric.

*Chaetotaxy.*—Elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

*Head.*—Genae smooth. Eyes prominent, convexity marked.

*Prothorax.*—Pronotum (Fig. 72). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, in contact with lateral margins.

*Pterothorax.*—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra.*—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex denticulate; sutural apex denticulate. Interneurs 2–6 continuous, shallow, impunctate. Discal and umbilical punctures not foveate.

*Hind Wings.*—(Fig. 78) Macropterous.

*Legs.*—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia.*—Median lobe in dorsal aspect (Fig. 93A, 94A) with apical portion very short; apex acute, narrowly to moderately broadly rounded; in left lateral aspect (Fig. 93B, 94B) apical portion narrow, apex acute. Internal sac (Fig. 98) markedly elongate; basal and preapical lobes absent; armature about 17 short, broad spinose sclerites, in two rows—one row extended prebasally to preapically, mainly ventral, one row mainly dorsal; without basal spinose sclerites.

*Ovipositor.*—(Fig. 105) Styломere 2 form 3.

### Variation

The name *O. dimidiata* represents a distinctive color phase of *O. tricolor* in western and central Mexico (pale morph, Fig. 109), with specimens from Sonora and Chihuahua to the southern end of the Sierra Madre del Sur in Oaxaca on the Pacific Versant tending to have about the basal 60% of the elytron pale with the contrast abrupt. Specimens from eastern and southern Mexico and Central America (nominotypical *O. tricolor*, the dark morph, Fig. 109) tend to have only about the basal 40% of the elytron pale, with the color demarcation gradual. However, some specimens from central Mexico (Tenancingo, in the Transvolcanic Sierra) and in the Sierra Madre del Sur (Cacalutla, Marquelia) are intermediate. Furthermore, there are no differences in other features (such as male genitalia) that correlate with the color differences.

We use the epithet “*dimidiata*” as an informal designation for the paler western Mexican color form. The name is available for formal use and is senior to the epithet *apicalis*.

### Habitat

Adults of this species are encountered in vegetation formations ranging from deciduous thorn forest to pine–oak, and in altitude extending from near sea level to about 2300 m. Many specimens were taken at UV light traps at night, most of them from May to October. Although adults are found in bromeliads from December to April, the species is a much less conspicuous part of the dry season bromeliad fauna than are some related species, notably *O. fulgens*.

### Geographical Distribution

The range of this species extends from Venezuela northward in western Mexico on the western slopes of the Sierra Madre Occidental to southern Sonora and Chihuahua, and in eastern Mexico along the Atlantic flanks of the Sierra Madre Oriental, to southern Tamaulipas (Fig. 109).

### Chorological Affinities

The widest-ranging species of the genus, the range of this species overlaps those of virtually every other species of *Onypterygia*. This is true also of the species to which *O. tricolor* is most closely related, *O. hoepfneri* and *O. sallei*.

### Material Examined

About 1400 specimens of *O. tricolor* were seen by us, from the following localities.

**MEXICO.** **Chiapas:** 1 male, 1 female, 2 km S Chicosen, road to Mirador, VI.18.1989, H. F. Howden (UASM); 1 male, Cinco Cerros, 860 m, V.31.1990, H. & A. Howden (UASM); 4 specimens, 50–52 km SE Comitán, U-V light (TAMU, UASM); 1 male, 1 female, El Chorreadero, 8 km E Chiapa de Corzo, V.17.1989, H. F. Howden (UASM); Escopetazo, jct. Hwy. 190 & 195; 1 male, 7.4 km N Frontera Comalapa, U-V light, VI.17.1966, Ball and Whitehead (UASM); 1 female, 32.2–40.2 km N Huixtla, VI.30.1969, H. J. Teskey (CNCI); 1 male, Jaltenango, El Triunfo, V.12.1985, H. Velasco (UNAM); 1 male, 3.2 km W Lazaro Cardenas, VI.26.1969, J. M. Campbell (CNCI); 1 specimen, 1 km E Navenchauc, bromeliads, I.13 (UASM); 1 male, Parque El Aguacero, 16 km W Ocozocoautla, VI.9.1989, H. F. Howden (UASM); 1 female, same, VI.24.1989 (UASM); 1 specimen, 13 km E Rizo de Oro (UASM); 1 male, Ruinas Chincultic, 1500 m, VI.30.1990, B. D. Gill (CMNC); 1 male, 2 females, San Cristobal de las Casas VI.7, H. F. Howden (CNCI); 1 male, 32.2 km W San Cristóbal de las Casas, V.20.1969, J. M. Campbell (CNCI); 11.3 km E Simojovel (CISC); 1 male, 13 km S Simojovel, jct. Hwys. 190 & 195, VI.10.1969, J. M. Campbell (CNCI); 2 females, same, VI.6.1969 (CNCI); 1 male, 2 females, 27.4 km SE Teopisca, VI.3–4, H. F. Howden (CNCI); 1 male, 1 female, 125.5 km W Tuxtla Gutiérrez, VII.27 (CISC). **Chihuahua:** 2 specimens, 6.4 km N Las Chinacas (nr. Sonora border), 1494 m, VII.9–10.1989, S. McCleve (UASM). **Colima:** 1 female, 42 km SW Colima (MCPM); 14.5–16.0 km NE Comala (TAMU); 30 males, 26 females, Tecuiztlan, VII.26.1967, Ball, T. L. Erwin and R. E. Leech (UASM); 10 males, 2 females, Volcan de Colima (USNM). **Guerrero:** 1 male, Apipiluleo (USNM); 1 female, 5.3 km N rd. to Buenavista de Cuellar (USNM); nr. Caca-huamilpa (TAMU); 9.7 km SE Cacalutla (TAMU); 1 male, Chilpancingo, VII.23 (CISC); 1 male, 29 km N. Chilpancingo, VII.18 (UCDC); 1 female, Km 95, Coyuca-Zihuatanejo, VII.25.1985, F. Arias & Y. Barba (UNAM); 1 female, Ixcuinatoyac, IX.10 (USNM); 6.0 km E Marquelia (TAMU); 3 specimens, 8 km S Mazatlán, Hwy 95, 1130 m, VI.29.1992, C. Bellamy (CMNH); 1 male, 1 female, 12.6 km S Mazatlán, VI.28 (USNM); 2 specimens, 2.5 km S Milpillas, Hwy. 95, VII.17.1992, C. Bellamy (CMNH); 4 specimens, 7 km N. Milpillas, 600 m, VI.30.1982, J. E. Rawlins (CMNH); 1 male, 2.5 km S Taxco, 1800 m, IX.19.1989, R. Turnbow (RHTC). **Hidalgo:** 2 males, 1 female, El Barrio, VI.18 (UASM); 1 male, 38.3 km NE Jacala, XI.13.1965, Ball and Whitehead (UASM). **Jalisco:** 2 males, Ajijic nr. Atenquique, VII.16–18 (USNM); 25.7 & 32.2 km SW & 16 km N. Autlán (CDAE, CASC, TAMU); 1 male, Chapala, VII.8 (CISC); 1 male, 9.7 km W Chapala, VI.20.1963, J. Doyen (CNCI); 5 specimens, 15 km W El Texquequite, 1046 m, VI.30.1977, J. E. Rawlins (CMNH); 1 male, 3 females, Guadalajara, VII.17–20.1967, Ball, T. L. Erwin, and R. E. Leech (UASM); 27 km N Guadalajara (TAMU); 1 male, 16.1 km E Ixtlán del Río, VIII.10 (MCPM); 1 specimen, Jamay (TAMU); 1 male, 33.2 km NW Magdalena, VII.30 (CISC); 2 specimens, 25.7 km SW Mazamitla (CDAE); 2 specimens, 5 km SE Plan de Barrancas (UCDC); 1 specimen, 19.3 km W Poncitlán (TAMU); 1 specimen, 34.9 km S Puerto Vallarta (CDAE); 1 specimen, San Sebastián, Sierra Madeiro, Sierra Madeiro Mts (CASC); 1 specimen, 52.3 km S Tecalitlán (UASM); 1 male, 4 females, 8.8 km NE Tecolotlán (CDAE); 6 males, 8 females, Volcán Tequila, 10–14 km SSW Tequila, XI.8.1974, D. E. & J. A. Breedlove (CASC). **Méjico:** 2 males, 3 females, Temascaltepec, (CASC); 6.4 km S Tenancingo, bromeliads, IV.22.1966 (UASM). **Michoacán:** 2 males, 87.1 km W Apatzingan, road to Dos Aguas (UASM); 2 females, Atzimba Nat. Park, III.25 (UCDC, USNM); 1 female, 17.7 km S Tzitzio, on Huetamo rd., 19°20'N, 100°50'W, VII.10.1947, T. H. Hubbell (UMMZ); 1 specimen, 24 km E Zamora, VIII.14 (UASM). **Morelos:** 2 specimens, Cañon de Lobos, Km 19 E Cuernavaca, 1120–1375 m, VII.3.1992, C. Bellamy (CMNH); 1 male, 3 females, Cuernavaca, 1676 m, H. E. Evans (CUIC); 11 males, 9 females, 6.4 km E Cuernavaca, 1829 m, VI.6–23.1959, H. E. & M. A. Evans (CUIC); 11 males, 9 females, 8.4 km E Cuernavaca, U-V light, VI.23–30. 1966, Ball and Whitehead (UASM); 1 female, 11.3 km E Cuernavaca, VII.15.1969, J. M. Campbell, D. E. Bright (CNCI); 5 males, 1 female, Huejintlán, VII.21, VIII.22 (UASM); 2 females, Puente de Ixtla (UASM); 1 male, 1 female, near Tijalpa (UASM); 1 male, Tequesquitengo, VII.15 (UASM); Xochicalco; Yautepec (UCDC). **Nayarit:** 3 females, Ahuacatlán, nr. Compostela, VII.18–22 (UASM); 12 males, 16 females, 11 km E Compostela, Rte. 68D, 1250 m, U-V light, VII.23 (UASM); 1 male, 1 female, El Pichón, VI.25 (CISC); 6 males, 2 females, Jesus Maria, VII.6–27 (CISC); 16 males, 16 females, La Mesa de Nayar, VII.19–21 (CISC); 2 specimens, 57.9 km SW Las Piedras (UASM); San Blas (FSCA, USNM); 4 males, 5 females, San Juan Peyotán, VIII.2 (CISC); 6 males, 3 females, Tepic, VIII.7 (CISC); 4 males, 3 females, Tepic (UASM); 4 specimens, 23 km S Tepic, 1070 m, VII.17.1977, J. E. Rawlins (CMNH); 1 specimen, 29.0 km S Tepic (TAMU); 2 females, Volcán Ceboruco, 8–12 km N. Jala, X.4.1990, J. E. Wappes (JEWG); 1 male, same, 4.9 km S Jala, X.7.1992, R. Turnbow (RHTC). **Oaxaca:** 3 males, 3 females, Juchatengo VII.19.1966, U-V Light, Ball and Whitehead (UASM); 82.5 km S Juchatengo (UASM); 2 males, La Ventosa, 115.8 km E Oaxaca, J. Doyen (CISC, CUIC); 4 specimens, 6 km E

Pinatepa near river, 180 m, VIII.16.1986, J. Rawlins, R. Davidson (CMNH); 1 female, 10 km E Tapatepec (UASM); 8.0 km W Tehuantepec; 1 female, 71 km W Tehuantepec, VII.21 (CISC); 2 males, 1 female, 9.7 km S Valle Nacional, V.18.1971, D. E. Bright (CNCI). **Puebla:** 1 female, near Tepexco, IX.5.1965, Ball and Whitehead (UASM). **San Luis Potosí:** 1 male, El Naranjo, VI.29.1966, Ball and Whitehead (UASM); 1 specimen, El Salto (FSCA); 1 male, 1 female, El Salto falls, 12 km NW El Naranjo, 400 m, U-V light, VII.2.1990, J. S. Ashe, K. J. Ahn, R. Leschen (SEMC); 1 male, same, VII.4.1990, R. L. Minckley (SEMC); 2 specimens, Puerto Verde, 64 km W Ciudad Valles (TAMU); 3 specimens, Tamán, ca. 16 km SW Tamazunchale (UASM); 1 male, Tamazunchale, VII.28 (UASM); 1 male, 29 km SW Tamazunchale VIII.2 (CISC); 2 females, Xilitla VII.21 (UASM); 1 specimen, 3.2 km E Xilitla (TAMU); 1 specimen, Hwy 70, km 82, microondas rd. jct (TAMU). **Sinaloa:** 61 km NE Concordia (CDAE, TAMU); 3 males, 4 females, Culiacán, VII.21.1959, H. E. Evans (CUIC); 9.7 km S Culiacán (CISC); 1 female, 16 km N. Mazatlán, VIII.7 (MCPM); 1 female, Microondas El Indio, Hwy. 15, 370 m, Sinaloan thorn forest, U-V light, 93.30, VII.18.1993, S. McCleve, G. E. & K. E. Ball (UASM); 2 males, Pánuco, intercepted with orchids (USNM); 1 male, Venedillo, VI.6 (CASC); 34 & 43 km E Villa Union, VII.25–26 (CISC). **Sonora:** 1 male, 91 km N Culican, VIII.28 (UCDC); 1 female, 5.1 km NW Huicoche, 1577 m, U-V light, VII.11–13.1989, S. McCleve (UASM). **Tamaulipas:** 1 specimen, 8.0 km SSE Gómez Farías (TAMU). **Veracruz:** 1 female, Acayucan, X.23 (UASM); 19.3 km NW Amate (TAMU); 13–16 km NE & 34 km S Catemaco (CISC); 10 specimens, Córdoba (CISC); 115 specimens, Cotaxtla (CISC); 19 specimens, 7.2 km NE Coscomatepec, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); 1 female, Cuitlahuac (USNM); 6 males, 4 females, Dos Amates, VII.16–17.1969, D. E. Bright, J. M. Campbell (CNCI); 1 male, Fortín de las Flores, VI.29.1964, A. G. Raske (CNCI); 0–3.2 km W Fortín de las Flores, bromeliads, III.7 (CISC); 8 km N, 11.3 km NE, & 32.2 km NW Huatusco (UASM); Jalapa (UASM, USNM); 1 female, 2.5 km S Jalapa, 1370 m, light, V.28.1991, J. S. Ashe (SEMC); 5 males, 1 female, 10 km NW Jalapa, bromeliads, IV.8.1966, Ball and Whitehead (UASM); 1 female, La Tinaja, VII.27 (UASM); Lake Catemaco (FSCA, TAMU); 1 male, Nacimiento de Río Atojal, VII.13.1966, Ball and Whitehead (UASM); Orizaba (CASC, MCPM); 1 female, 4.8 km NE Orizaba, 1219 m, IX.3.1959, I. J. Cantrall, T. J. Cohn (UMMZ); 1 male, Presidio, VII.30 (USNM); 1 female, Río Blanco, IX.13 (UASM); 40 specimens, San Andres Tuxtla, IV.27 (USNM); 1 female, 11.3 km N. Santiago Tuxtla, VII.8.1963, J. Doyen (CNCI); 9 males, 1 female, 4 km W, 10.6 km E Sontecomapan, VI, VII, IX (UASM); 3 males, 9.7 km S Sontecomapan, Clark & Cave (AUEM); 2 females, 8 km S Sontecomapan, IX.7.1982, Clark & Cave (AUEM); 1 female, Tuxpango–Orizaba, VIII.13 (USNM); Veracruz. **BELIZE. Cayo District:** 1 specimen, Chiquibul River, VI.21–23.1985, Ellen Censky (CMNH). **COSTA RICA. Alajuela:** 1 specimen, Alajuela (USNM). **Guanacaste:** 3 specimens, Bebedero, VI.13, VII.4 (USNM); 1 specimen, Hacienda Palo Verde (USNM); 1 specimen, La Pacifica, nr. Cañas (JEWC); 1 female, Maritza Biological Stn., Parque Nacional Guanacaste, V.21.1993, D. Brzoska (SEMC); 3 specimens, Santa Rosa National Park (USNM). **Puntarenas:** 1 specimen, 6 km S Santa Elena (JEWC); 1 male, 2 females, Monteverde area, VI.4–6.1980, J. E. Wappes (UASM); 1 male, Monteverde, U-V light, V.7–12.1989, E. Fuller (UASM); 1 female, same, V.25 & 28.1979; 5 males, 3 females, same, U-V light, V.10.1989, J. S. Ashe, R. Brooks, R. Leschen (SEMC); 1 male, 4 females, same, 1550 m, V.24.1989; 1 female, same, flight intercept trap, 1570 m, V.14.1989; 1 male, Monteverde, Cerro Amigas, ex leaf litter at base of tree, 1785 m, V.22.1989; 1 male, 2 females, Monteverde, Pension Quetzal, VI.5.1992, F. Andrews & A. Gilbert (CDAE). **San José:** 4 specimens, Atenas (MCZC, USNM); 3 specimens, San José (USNM). **EL SALVADOR.** 1 male, Cerro Verde, 2000 m, V.1.1971, H. F. Howden (UASM); 1 specimen, Landaverde (FSCA). **La Libertad:** 76 specimens, Boquerón (CNCI); 2 specimens, Los Chorros (FSCA); Quetzaltepeque (UCDC); 2 specimens, 4.0 km and 4.8 km S Quetzaltepeque (USNM); 3 specimens, Santa Tecla (FSCA, USNM). **La Union:** 4 specimens La Union (USNM). **San Salvador:** 2 specimens, San Salvador, V.22 (USNM). **Santa Ana:** 2 specimens, 6 km W Hwy. CA 1, above Lago de Coatepeque, 853 m, VI.1 (USNM); Montecristo, 2300 m (FSCA, USNM); 4 males, 2 females, Monte Cristo, 2300 m, V.9.1971, H. F. Howden, S. B. Peck (UASM). **GUATEMALA. Alta Verapaz:** 1 specimen, 22.2 km W La Tinta. U-V light (USNM); 1 specimen, Panzós (MCZC). **Chimaltenango:** 2 specimens, S. P. Yepocapa (USNM). **Escuintla:** 3 specimens, Zapote (FMNH). **San Marcos:** 1 specimen, 17.3 km SE Talisman, Río Cabús (USNM). **Suchitepéquez:** 1 male, Finca El Ciprés, VI (CASC). **Zacapa:** 1 female, 3 km E La Union, VI.6.1991, H. F. & A. Howden (UASM); 1 female, Sierra del Espíritu Santo, 3 km SE Limón, tropical montane forest, beating vegetation, 1400–1500 m, VI.6.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 2 females, same, but at U-V light. **HONDURAS. Copán:** 1 male, 1 female, 19 km SW Sta. Rosa de Copán, X.8.1993, R. Turnbow (RHTC). **El Paraíso:** 17 km NW Jacaleapa, X.12.1993, R. Turnbow (RHTC); 1 male, Cerro Montserrat, 7 km SW Yuscarán, 1800 m, V.21.1994, H. & A. Howden (UASM). **Federico Morazán:** 1 male, 3 females, Cerro Uyuca, 30 km E Tegucigalpa, 1800 m, V.16 & 19.1994, H. F. & A. Howden (UASM); 2 specimens, nr. Tegucigalpa (FSCA); 4 specimens, Zamorano (UMMZ). **Olancho:** Parque Nacional La Muralla, V.24–

VI.1.1995, R. H. Turnbow (RHTC). **NICARAGUA.** Managua. **Rivas:** 1 specimen, Río Canas Gordas, km 133, bet. La Virgena & Sapoá (FSCA); 1 female, Leon, VI.1989, J. M. Maes (UNAN); 1 male, Grenada v. Mombacho, VII.1989, F. Reinholdt (UNAN). **PANAMA.** 2 specimens, Santa María El Real (MCZC). **Coclé:** 1 specimen, El Valle (USNM). **Panama:** 1 specimen, Cerro Campana, Hespenheide (USNM); 1 female, Cerro Azul & Cerro Jefe at standing lights, V.11.1991, R. H. Turnbow (RHTC); 1 specimen, 80 km E Chepo (USNM). **VENEZUELA.** Aragua: 4 males, 1 female, Rancho Grande, V.15.1973, G. Ekis (USNM).

*Onypterygia hoepfneri* Dejean  
(Fig. 1; 3; 9; 73; 79; 95A, B; 99; 106; 110)

*Onypterygia hoepfneri* Dejean, 1831:347. Lectotype (here designated) male, labelled: "Höpfneri in Mexico" [green paper]; "D. Höpfner" [green paper]; "Ex Musaeo/Chaudoir" [red print]. Castelnau, 1840:42. Bates, 1882:130. Heyne, 1895:25.

*Onychopterygia hoepfneri*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

#### Type Locality

Type area Mexico, type locality here restricted to 8.7 km east of Cuernavaca, state of Morelos.

#### Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Large in size, with submetallic to metallic green or blue fore body, and markedly alutaceous maroon elytra, adults of *O. hoepfneri* are distinguished from those of the closely related, allopatric *O. sallei* by having inconspicuous preapical elytral calli, and less distinctly punctate posterolateral pronotal impressions.

#### Description

With diagnostic combination of *O. hoepfneri* and the following.

**Habitus.**—As in Figure 1.

**Measurements and Proportions.**—TL intermediate to large (13.0–17.5 mm), WP/WH low (1.24), LP/WP intermediate (0.82), WP/WPb low (1.16), LE/WE intermediate (1.73).

**Color.**—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous, maroon. Femora metallic, partially black; tibiae and tarsi piceous-black.

**Microsculpture, Mesh Pattern.**—Head, isodiametric; pronotum, microlines effaced, surface smooth; elytra (Fig. 3), isodiametric.

**Chaetotaxy.**—Pronotum, lateral setae one pair; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

**Head.**—Genae smooth, not rugose. Eyes prominent, convexity marked.

**Prothorax.**—Pronotum (Fig. 73). Anterior bead complete; lateral beads absent anteriorly, evident posteriorly. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

**Pterothorax.**—Mesepisternum partially punctate. Metepisternum elongate.

**Elytra.**—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex angulate; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures not foveate.

**Hind Wings.**—(Fig. 79) Macropterous.

**Legs.**—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

**Male Genitalia.**—(Fig. 95A, B; 99) Median lobe in dorsal aspect with apical portion short; apex broadly rounded; in left lateral aspect (Fig. 95B), apical portion slender, apex acute. Internal sac (Fig. 99) markedly elongate; basal and preapical lobes absent; armature of 28 spinose sclerites, as follows—three in basal group (one dorsal, one left ventral, and one left ventral), remaining in two rows (one dorsal, one ventral), extended from prebasal area to apex.

**Ovipositor.**—(Fig. 106) Styломere 2 form 3.

### Variation

Although we consider *O. sallaei* from Veracruz distinct from *O. hoepfneri* to the south and west, we are not satisfied fully that these are distinct species. The two taxa are closely related and may prove to be linked by intermediates (as has been found for *O. thoreyi* and *O. fulgens*, see above), and in this discussion, we consider them together. Both forms were recorded by Bates (1882:130) from Juquila, but the record of *O. sallaei* is based on a specimen of *O. hoepfneri*, and it seems that *O. sallaei* lives only in central Veracruz.

Available samples of *O. hoepfneri* and *O. sallaei* form four geographical clusters of more or less recognizable forms: central Mexico (Guerrero, Jalisco, México, Michoacán, and Morelos), the Sierra Madre del Sur of Oaxaca, Chiapas-Honduras, and central Veracruz (*O. sallaei*). Character states of the Oaxaca specimens are intermediate between those from Chiapas and central Mexico.

The Veracruz morph seems both disjunctive and distinctive, but nonetheless more similar to *O. hoepfneri* from Chiapas than from Oaxaca or central Mexico. Most readily observed variables seem to form clines from central and western Mexico, south to Chiapas, and north in the east to central Veracruz. The most distinctly marked of these are elytral color (more greenish toward Veracruz), numbers of ambulatory setae on abdominal sterna IV-VI (increasing toward Veracruz), number of spinose sclerites on the internal sac (decreasing toward Veracruz), width of lateral margins of pronotum (broadest in Veracruz), color of fore body (most markedly metallic in Veracruz), and form of elytral apex (most markedly produced and angulate in Veracruz).

However, we consider the allopatric *O. sallaei* distinct from *O. hoepfneri* because its known distribution is disjunctive and available specimens are distinguishable at a glance. *Onypterygia hoepfneri* has much more markedly alutaceous and hence less brilliantly colored elytra than does *O. sallaei*. The elytra characteristic of the latter species have rather marked preapical calli, and these are lacking from or inconspicuous in *O. hoepfneri*. In *O. sallaei*, the pronotal posterolateral impressions are markedly, densely punctate; in *O. hoepfneri*, these impressions are much more finely and less distinctly punctate. Another discontinuity is in size: the Veracruz specimens smaller, and those from Chiapas larger.

No evident geographical variation was found in numbers of posterior marginal setae of abdominal sternum VII. In 40 males of *O. hoepfneri* and three of *O. sallaei*, the number of setae ranged from 22 to 33, sample means 26.3 to 27.2.

This lack of differentiation contrasts with variation observed in total numbers of paramedian ambulatory setae on abdominal sterna IV-VI: female sample means 6.0, 6.7, 9.3, and 12.0, and male means 6.0, 6.0, 7.2, and 8.0, in central México, Oaxaca, Chiapas, and Veracruz, respectively.

### Habitat

Adults of this species have been collected in bromeliads (January through May), on foliage (August), and at UV light traps (June, July), at middle elevations from 1000 to about 2100 m altitude, in tropical deciduous thorn forests, oak forests, pine-oak forests, and montane rain forests.

### Geographical Distribution

The range of this species extends from El Salvador and Honduras northward to Jalisco Sinaloa in the Sierra Madre Occidental (Fig. 110). It is not known from Veracruz.

### *Chorological Affinities*

As noted above, this species and its putative adelphotaxon are allopatric. More generally, the range of *O. hoepfneri* overlaps the ranges of most of the other species of *Onypterygia*.

### *Phylogenetic Relationships*

This species and *O. sallaei* are postulated to be adelphotaxa. For details see the "Variation" section above.

### *Material Examined*

We have seen about 175 specimens of *O. hoepfneri* from the following localities.

**MEXICO.** **Chiapas:** 1 female, 65 km E Bochil, IX.13.1981, Clark & Coe (AUEM); 1 female, NW slope Baul, W. Rizo de Oro, 1768 m, X.12.1979, D. E. & J. A. Breedlove (CASC); 1 male, Cerro Bola, N Cerro Tres Picos, 1500–2100 m, V.5.1972, D. Breedlove (CASC); 2 females, nr. Chiapa de Corzo, jct. Hwy. 190 & 195, VI.24 (USNM); 3 males, 2 females, 47.8 km N. Huixtla, 1311 m, in bromeliads, II.26.1966, Ball and Whitehead (UASM); 1 female, Parque Nacional de Laguna de Montebello, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 1 male (teneral), same, Dos Lagos, on rd. to Santa Elena, 1219 m, D. E. & J. A. Breedlove (CASC); 1 female, Pueblo Nuevo, 1547 m, in bromeliads, V.25.1966, Ball and Whitehead (UASM); 2 males, 5.0 km S Pueblo Nuevo, 1646 m, in bromeliads, IV.27.1966, Ball and Whitehead (UASM); 1 male, Puerto Cate, IX.9.1981, Clark & Coe (AUEM); 12.7 km S Tapilula, 1463 m, cloud forest, VII.7.1966, Ball and Whitehead (UASM); 17 km W Tuxtla Gutiérrez, 1006 m (FSCA). **Colima:** 3 males, 5 females, vic. El Terrero, Los Sauces rd., km 7–8, X.4.1992, R. H. Turnbow (RHTC). **Guerrero:** Taxco; 1 male, 16 km WSW Xochipala, 1770 m, VI.30.1982, J. E. Rawlins (CMNH). **Jalisco:** 1 female, San Sebastián, Sierra Madeiro (CASC); 52.3 km S Tecalitlán, 1570 m, VIII.4.1967 (UASM). **México:** 1 female, Ixtapan de la Sal, 1768 m, U-V light, VII.12.1966, Ball and Whitehead (UASM); 4 males, 8 females, Ixtapan de la Sal, in bromeliads, III.5 (USNM); 4 males, 4 females, Temascaltepec (CASC); 1 female, same, 1931, G. B. Hinton (UNAM); 2 females, same, II.9.1979, H. Brailovsky (UNAM); 1 specimen, E. Valle de Bravo, Río de Molino, 2300 m, oak–pine forest, in bromeliads, IV.21.1966, Ball and Whitehead (UASM); 2 males, 1 female, nr. Valle de Bravo, VIII.3.1962, G. E. Ball (UASM). **Michoacán:** 4 males, 1 female, 28.2 km E Morelia, 2134 m, I.11 and 20.1966, Ball and Whitehead (UASM). **Morelos:** Cuernavaca, V.11.1959, H. E. Evans (CUIC); 3 males, 3 females, 7 km, & 7.1–8.7 km E Cuernavaca, 1402–1768 m, Ball and Whitehead (UASM). **Nayarit:** 1 female, 23 km S Tepic, 1066.8 m, J. E. Rawlins (CMNH). **Oaxaca:** Juquila (BMNH); 1 female, 55.5 km N. Pochutla, 1433 m, III.19–20.1966, Ball and Whitehead (UASM); 1 female, Portillo del Rayo, X.18.1985, E. Barrera (UNAM); 10 males, 7 females, 30.7 km S Suchixtepec, 1372 m, in bromeliads, III.17.1966, Ball and Whitehead (UASM). **Sinaloa:** 1 male, 7 km NE La Capilla del Taxte, 1250 m, VI.27.1977, J. E. Rawlins (CMNH). **EL SALVADOR.** **Santa Ana:** 1 female, Monte Cristo, 2300 m, V.9.1971, Howden & Peck (UASM). **GUATEMALA.** **Alta Verapaz:** Panzós (MCZC). **Baja Verapaz:** 1 male, 5 km E Purulhá, 1530–1650 m, VII.22–24.1977, E. Fisher, P. Sullivan (CASC); 1 female, 8 km S Purulhá, 1660 m, ex under bark, VI.30.1993, J. S. Ashe and R. Brooks, #162 (SEMC); Sabo (MCZC); 2 males, Sabo (USNM). **Chimaltenango:** S. P. Yecocapa, 1463 m (FMNH). **Escuintla:** 1 male, 8 km N. San Vicente Pacaya, 1371 m, V.14.1966, J. M. Campbell (CNCI). **Quetzaltenango:** Cerro Zunil (MCZC); 3 males, 1 female, same (USNM); 1 female, Los Pirineos Santa María, 1371.6 m, V.17.1966, J. M. Campbell (CNCI). **Sacatepéquez:** Dueñas (MCZC); 2 males, Dueñas (USNM). **Totonicapán:** Volcán Santa María, 1500 m, VI.19 (USNM). **Suchixtepec:** 1 female, 2 km N. Finca Colimas Zunilito, 1828.8 m, V.6.1966, J. M. Campbell (CNCI). **HONDURAS.** **El Paraíso:** 1 male, Cerro Montserrat, X.3.1993, R. R. Turnbow (RHTC).

### *Onypterygia sallaei* Chaudoir (Fig. 16, 74, 96, 100, 110)

*Onypterygia sallaei* Chaudoir, 1863:255. Lectotype (here designated) male, labelled "Cordova"; "Mexico./Sallé Coll."; "Onychopterygia sallaei Chaud. . .Sallé"; "H. W. Bates/Biol. Centr. Amer." (MNHP). Bates, 1882:130.

*Onychopterygia sallaei*; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

### *Type Locality*

Córdoba, Veracruz, Mexico.

### *Diagnostic Combination*

With character states of the *O. fulgens* species group, restricted as follows. A large-sized member of the *O. fulgens* group, with metallic green fore body and shiny, only slightly alutaceous, coppery-green elytra, *O. sallei* adults are distinguished from those of the closely related *O. hoepfneri* by having conspicuous preapical calli, and much more markedly punctate posterolateral pronotal impressions.

### *Description*

With diagnostic combination of *O. sallei* and the following.

*Measurements and Proportions*.—TL large (13.5–15.0 mm), WP/WH low (1.31), LP/WP intermediate (0.73), WP/WPB low (1.19), LE/WE intermediate (1.74).

*Color*.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous to black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous. Femora metallic, partially black; tibiae and tarsi piceous to black.

*Microsculpture, Mesh Pattern*.—Head, with microlines partially effaced, isodiametric; pronotum, with microlines effaced, surface smooth; elytra, isodiametric.

*Chaetotaxy*.—Pronotum, lateral setae one pair; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–V with one pair each; sternum VI with two pairs; sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

*Head*.—Genae rugose, lines fine. Eyes prominent, markedly convex.

*Prothorax*.—Pronotum (Fig. 74). Anterior bead incomplete; lateral beads absent anteriorly, evident posteriorly. Posterolateral impressions densely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

*Pterothorax*.—Mesepisternum partially punctate. Metepisternum elongate.

*Elytra*.—Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex angulate; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures not foveate.

*Hind Wings*.—Macropterous.

*Legs*.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

*Male Genitalia*.—Median lobe in left lateral aspect (Fig. 96) with apical portion broadly triangular, short; apical portion very short; apex acute. Internal sac (Fig. 100), markedly elongate; basal and preapical lobes absent; armature of 16 spinose sclerites, as follows—basal group three (one ventral, two dorsal), and two apical groups of seven and six (ventral and dorsal rows, respectively).

*Ovipositor*.—(Fig. 16) Styломere 2 form 3.

### *Variation*

See discussion of this topic for *O. hoepfneri* above.

### *Habitat*

This species occurs in montane rain forests, in middle elevations (between 880 and 1100 m). Five dated specimen records are from April 27–28, at UV light trap; June 21–30; August 16; October 18; and November 25.

### *Geographical Distribution*

This species is known only from below the eastern flanks of Volcán Citlaltepetl (Orizaba), in central Veracruz (Fig. 110).

### *Material Examined*

We have seen 16 specimens of *O. sallei* from the following localities in Mexico.

**Veracruz:** Córdoba (BMNH, MNHP); 5 km NE Coscomatepec, 1128 m, cloud forest, VI.21.1966, Ball and Whitehead (UASM); 1 female, Fortín de las Flores (UASM); 1 female, same, U-V light, IV.27–28 (FSCA); 3.2 km W Fortín de las Flores, VIII.16 (CISC); Jalapa (BMNH, AMNH); 1 male, same, Instituto de Ecología, 1300 m, ex epiphytes, XI.25.1994 (FFPC); Río Blanco (UNAM).

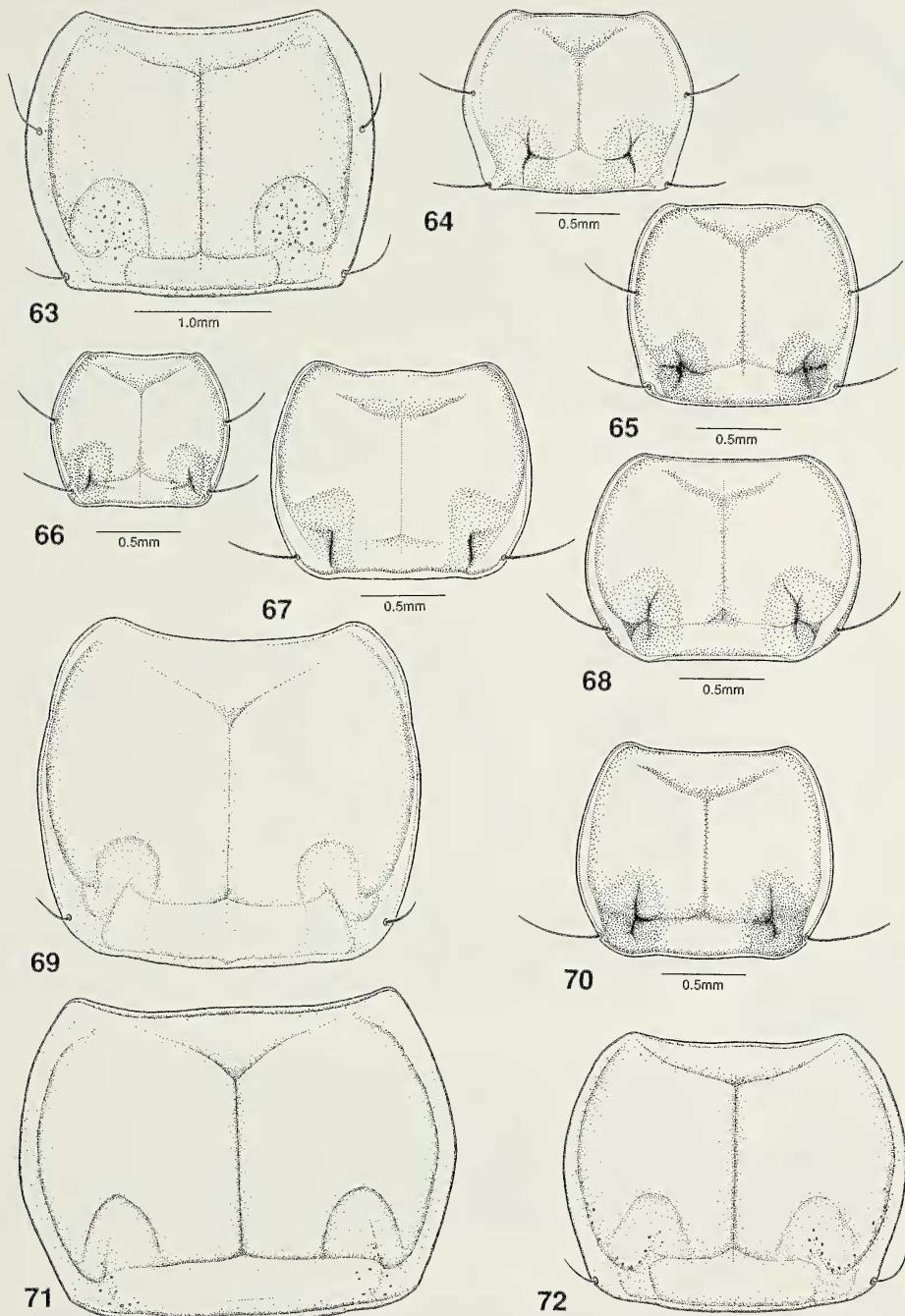


Fig. 63–72.—Line drawings of pronota, dorsal aspect, of species of the *O. fulgens* species group: 63, *O. iris* Chaudoir; 64, *O. championi* Bates; 65, *O. chrysura* Bates; 66, *O. kathleenae*, n. sp.; 67, *O. exeueros*, n. sp.; 68, *O. crabilli*, n. sp.; 69, *O. quadrispinosa* Bates (Guatemala); 70, same (Costa Rica); 71, *O. fulgens* Dejean; 72, *O. tricolor* Dejean.

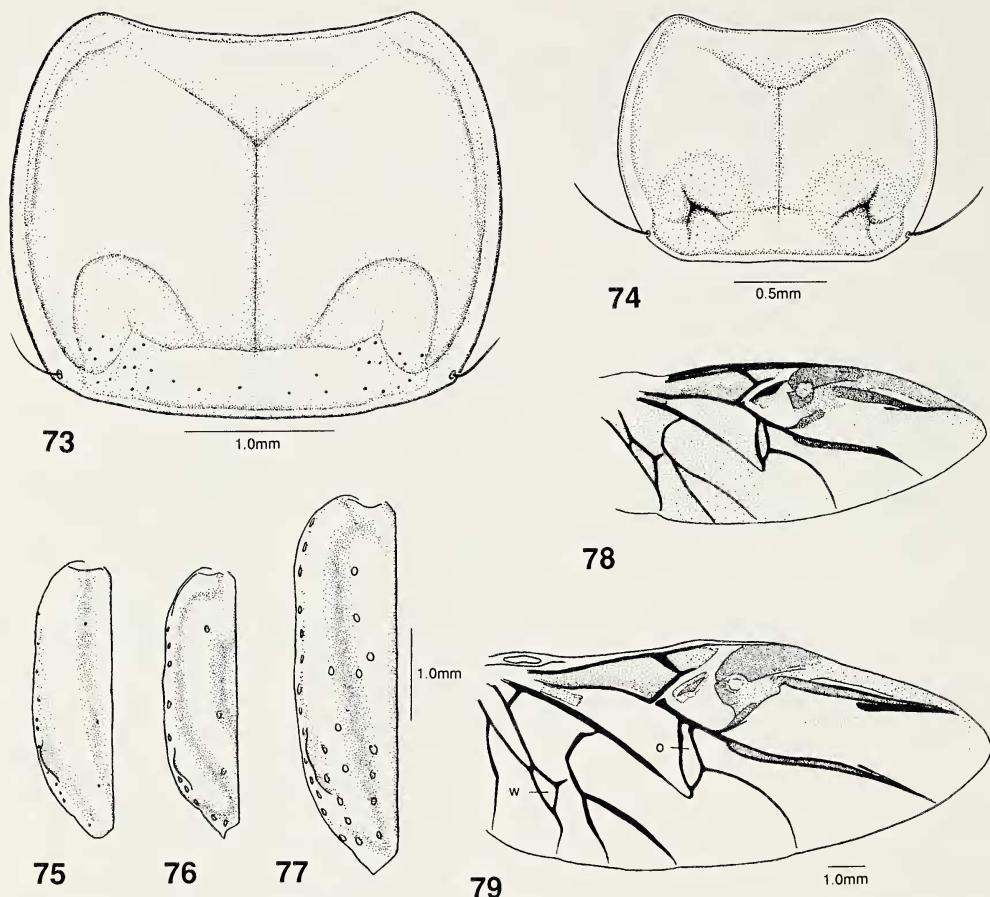


Fig. 73-79.—Line drawings of adult structural features of the *O. fulgens* species group. Fig. 73, 74, pronotum, dorsal aspect, of: 73, *O. hoepfneri* Dejean; 74, *O. sallei* Chadoir. Fig. 75-77, left elytron dorsal aspect, of: 75, *O. iris* Chadoir; 76, *O. championi* Bates; 77, *O. polytreta*, n. sp. 78, 79, left hind wing, ventral aspect of: 78, *O. tricolor* Dejean; 79, *O. hoepfneri* Dejean. Legend: o—oblongum cell, w—wedge cell.

#### ECOLOGICAL ASPECTS AND EVOLUTIONARY CONSIDERATIONS

##### *Ecological Aspects*

Data are not adequate for a detailed assessment of this subject. A few generalizations are sought, principally in the label data on specimens, which include limited information about: diel activity patterns, altitude occurrence and distribution, and habitat.

##### *Altitude*

Most species of *Onypterygia* are represented between 700 and 2000 m above sea level, with a few taxa known from higher altitudes only, and a few from lower (Table 4). However, the altitudinal ranges of *O. fulgens* and *O. tricolor* are very extensive (from sea level to 2300 m or more), and that of *O. fulgens* covers nearly the entire range of the genus. These latter two species have also the most extensive geographical ranges in *Onypterygia*.

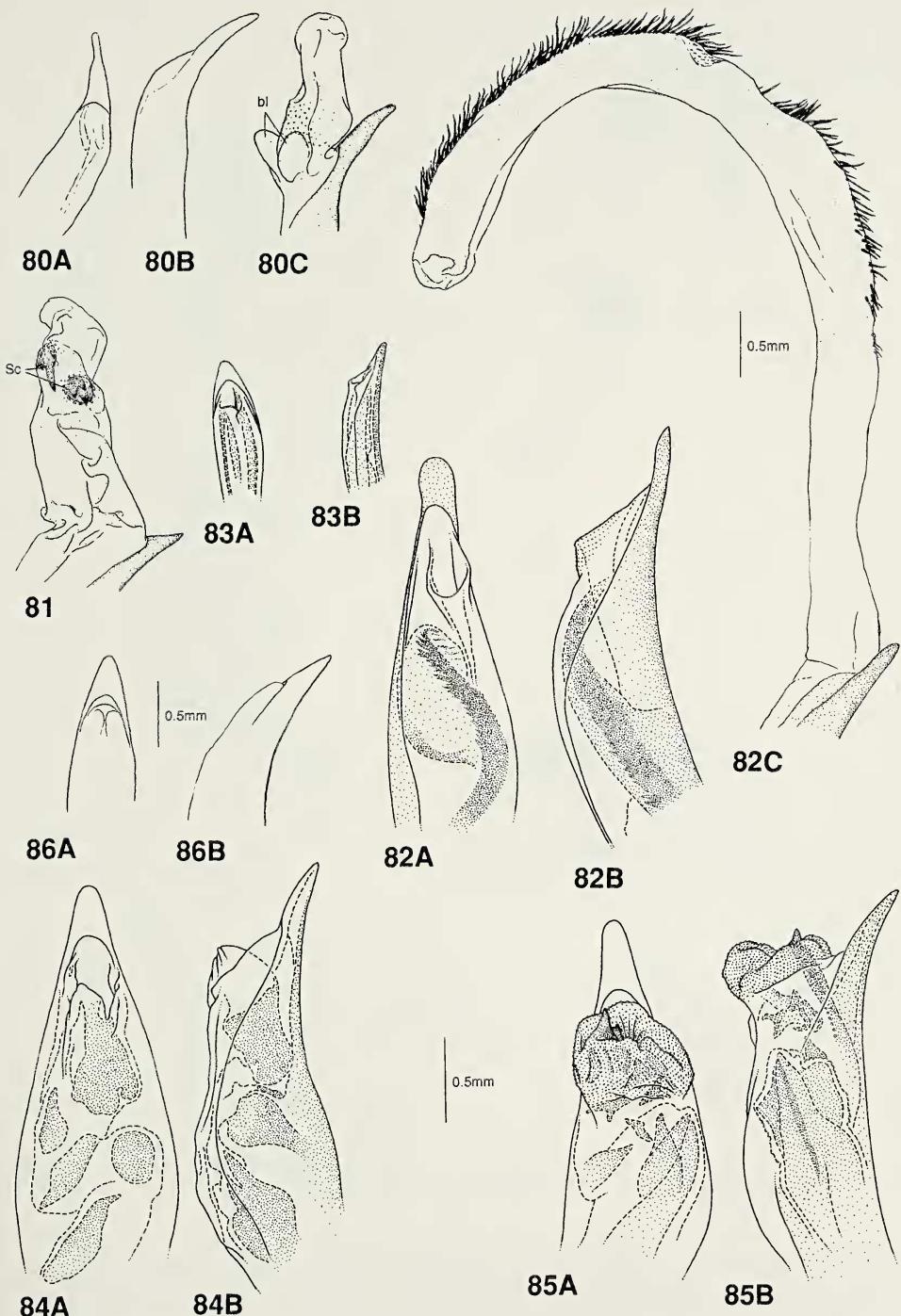


Fig. 80–86.—Line drawings of male genitalia of species of the *O. fulgens* species group: A, B, dorsal and left lateral aspects, respectively; C, left lateral aspect, with internal sac everted. 80, *O. iris* Chaudoir; 81, *O. championi* Bates; 82, *O. chrysura* Bates; 83, *O. kathleenae*, n. sp.; 84, *O. polytreta*, n. sp.; 85, *O. crabilli*, n. sp.; 86, *O. quadrispinosa* Bates. Legend: bl—basal lobes, Sc—spinose sclerites.

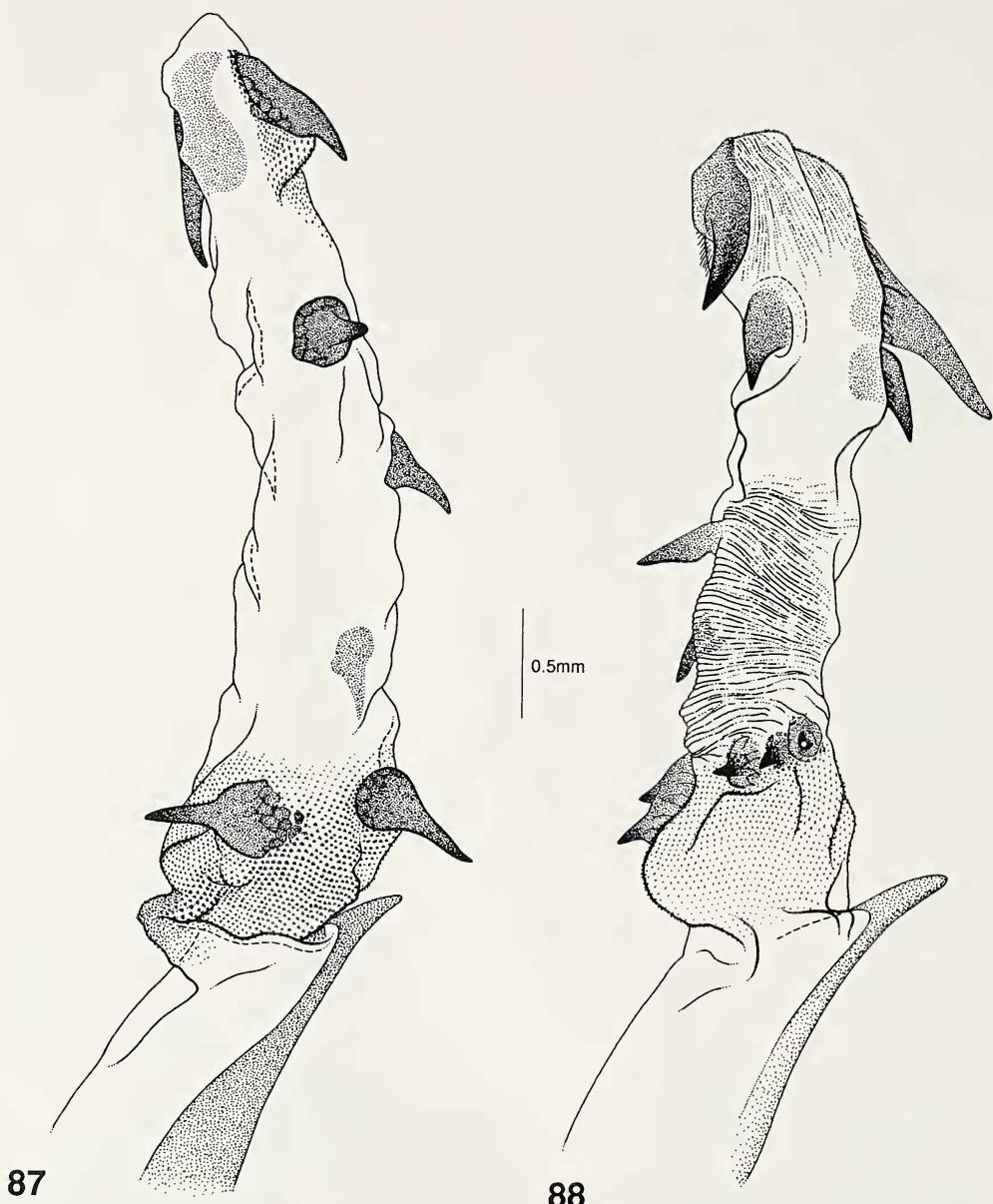


Fig. 87, 88.—Line drawings of median lobes of male genitalia, left lateral aspect, internal sac everted, of the *O. fulgens* species group: 87, *O. polytreta*, n. sp.; 88, *O. crabilli*, n. sp.

The correlated occurrence of two lineages (*wappesi* and *aeneipennis* species groups) at higher altitudes only (1400 m and above) and the brachypterous or wing-dimorphic condition of most of the included species (Table 4) is consistent with Darlington's observations (1971:165–172) based on study of New Guinea Carabidae, that flightlessness is selected for at such altitudes, and that the flightless species are the result of "conversion rather than concentration; that is, they have

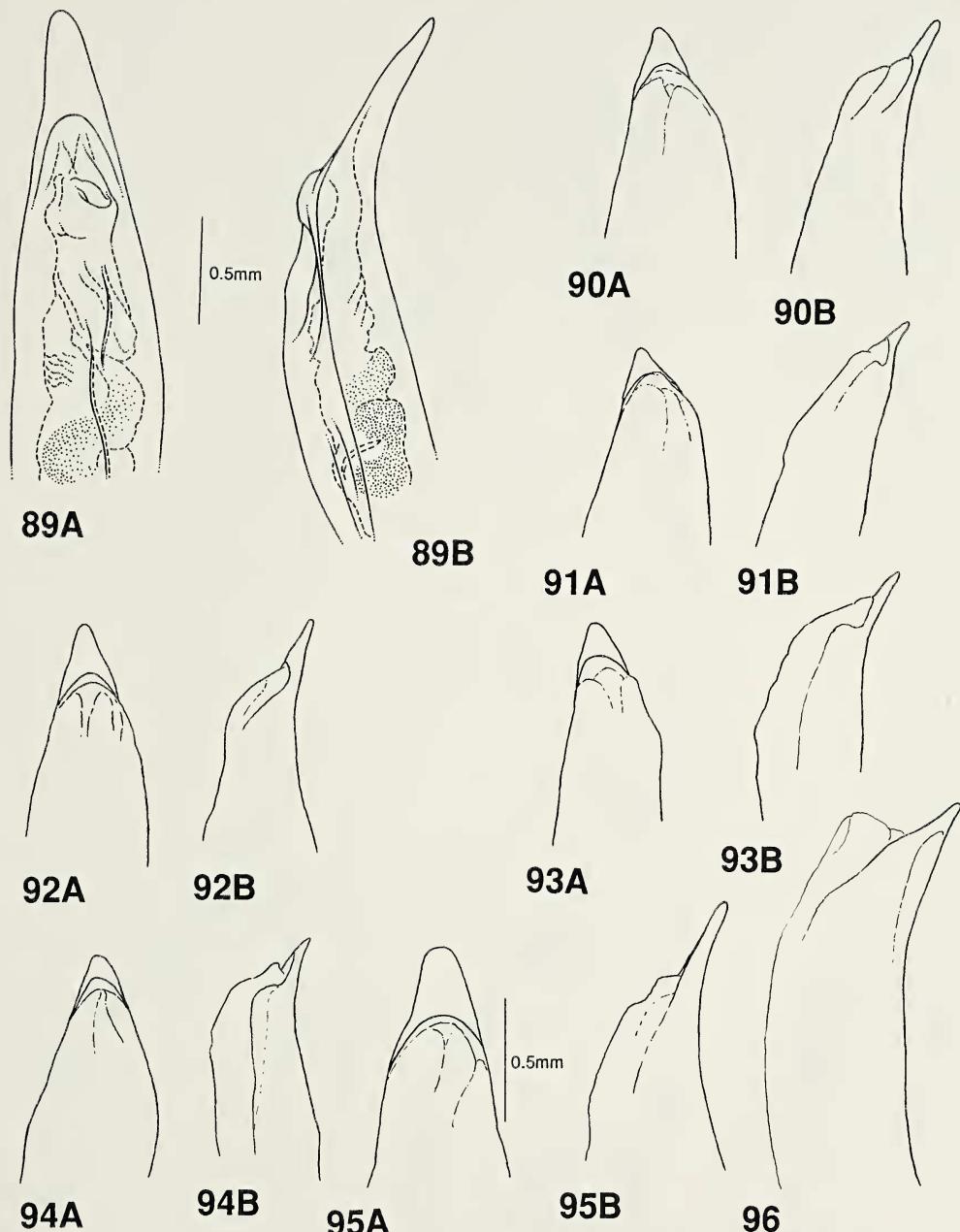


Fig. 89–96.—Line drawings of male genitalia of the *O. fulgens* species group. Fig. 89–95, median lobe, apical portion: A, B, dorsal and left lateral aspects, respectively, of: 89, *O. scintillans*, n. sp.; 90, *O. fulgens* Dejean (Orizaba, Veracruz, Mex.); 91, same (Landa de Matamoros, Queretaro, Mex.); 92, same (Tepic, Nayarit, Mex.); 93, *O. tricolor* Dejean (Jalapa, Veracruz, Mex.); 94, same (Juchatengo, Oaxaca, Mex.); 95, *O. hoepfneri* Dejean. Fig. 96, median lobe, apical portion, left lateral aspect, of *O. sallaei* Chaudoir.

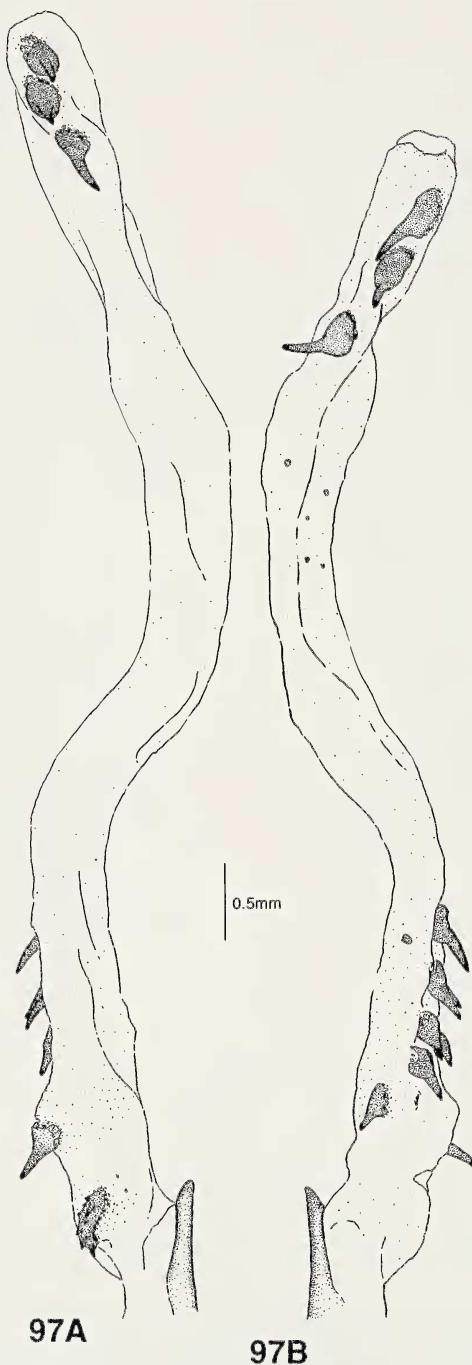


Fig. 97.—Male genitalia (median lobe, apical portion, with internal sac everted) of *Onypterygia fulgens* Dejean: A, left lateral aspect; B, right lateral aspect.

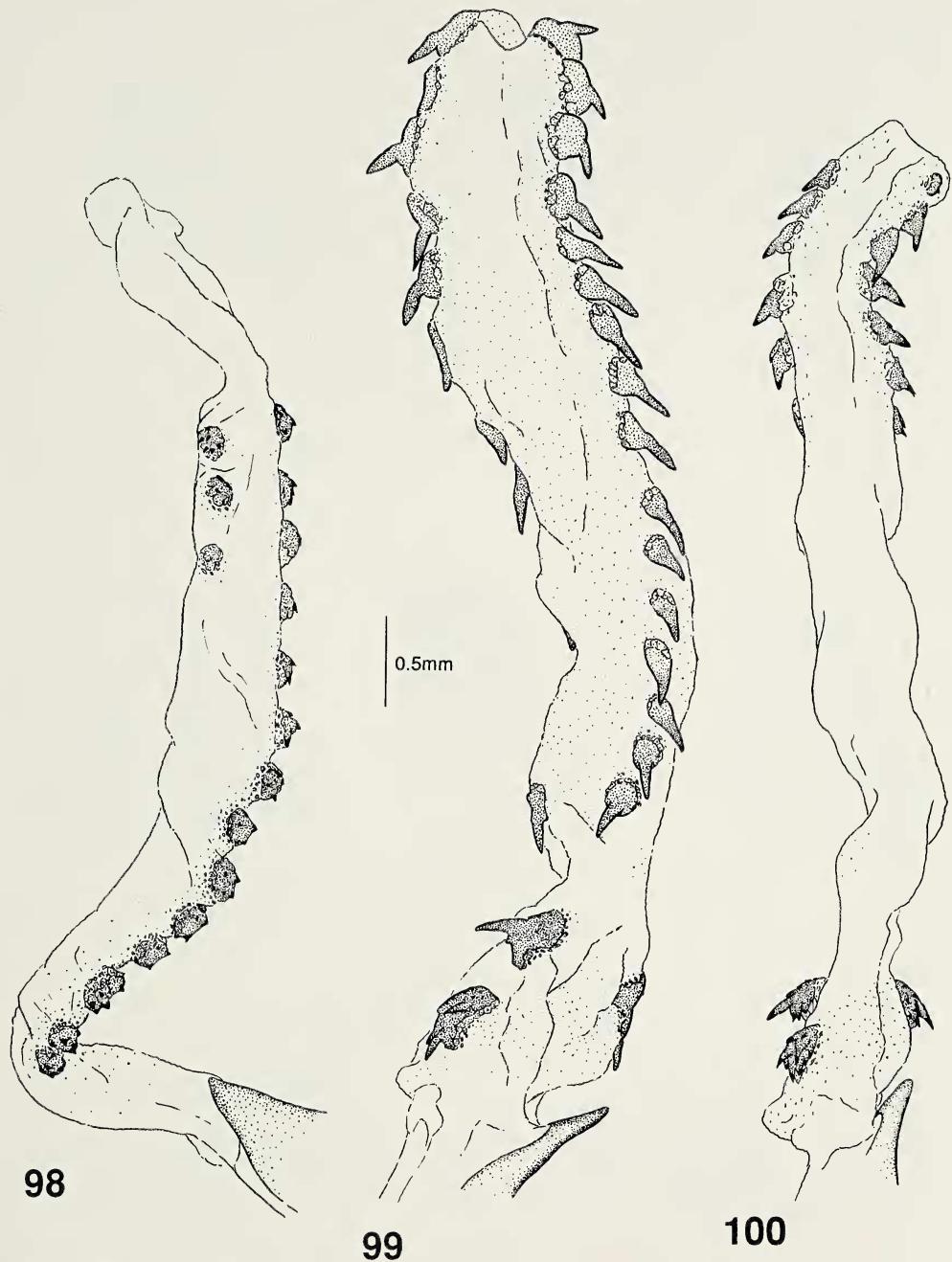


Fig. 98–100.—Line drawings of male genitalia (median lobe, apical portion, left lateral aspect, with internal sac everted) of species of the *O. fulgens* species group: 98, *O. tricolor* Dejean; 99, *O. hoepfneri* Dejean; 100, *O. sallaei* Chaudoir.

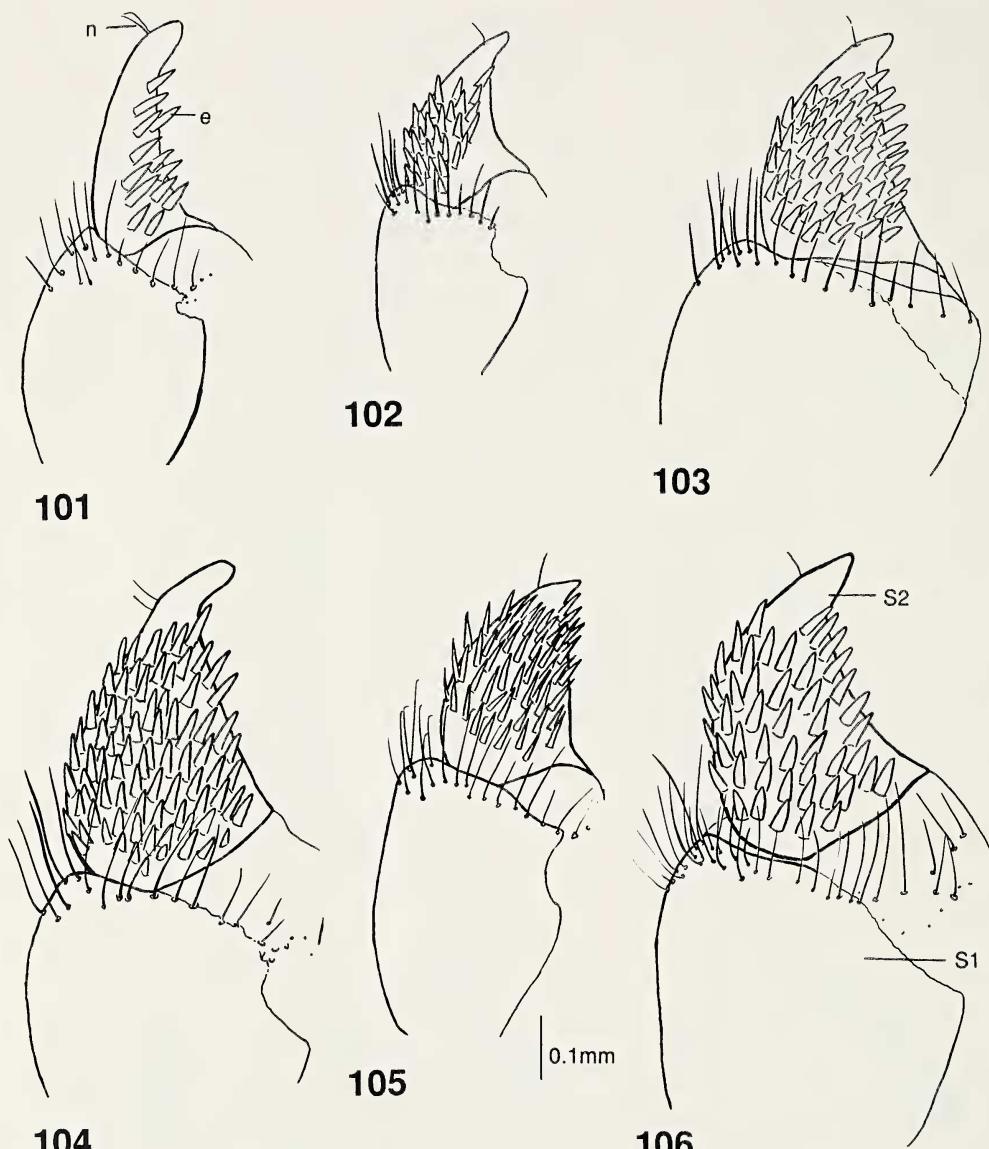


Fig. 101–106.—Line drawings of ovipositor sclerites (left stylomeres 1 and 2, left lateral aspect) of species of the *O. fulgens* species group: 101, *O. iris* Chaudoir; 102, *O. kathleenae*, n. sp.; 103, *O. polyptreta*, n. sp.; 104, *O. fulgens* Dejean; 105, *O. tricolor* Dejean; 106, *O. hoepfneri* Dejean. Legend: e—ensiform seta; n—nematiform seta; S1, S2—stylomeres 1 and 2, respectively.

been produced by atrophy processes that have occurred locally [i.e., within lineages] and not by accumulation of stocks with reduced wings from other regions" (Darlington, 1971:170; see also his more general treatment of wing loss [Darlington, 1943]). However, evolution of flightlessness by wing reduction occurred independently in each lineage because macroptery in the *aeneipennis* species group (*O. pallidipes*) implies a macropterous group ancestor, whereas the bra-

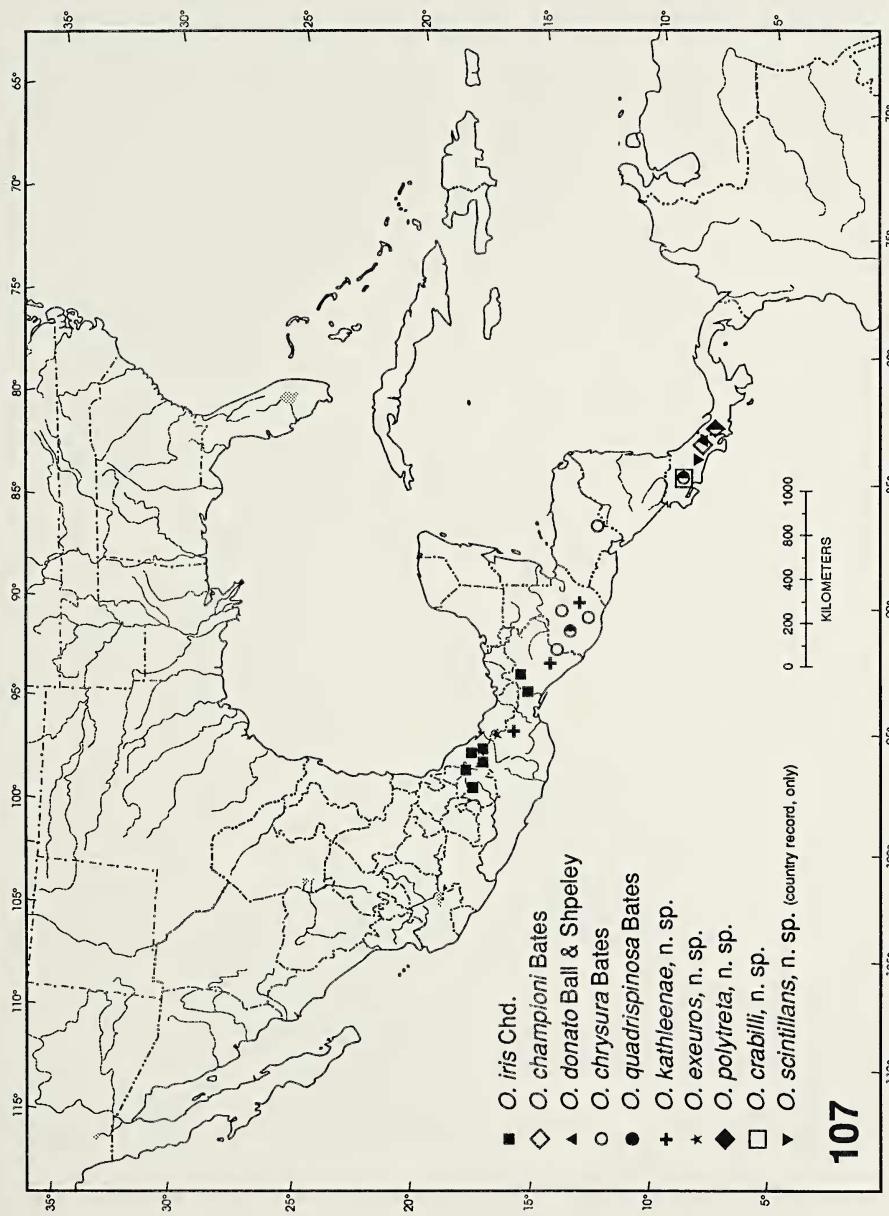


Fig. 107.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for species of the *O. fulgens* species group, except *O. fulgens* Dejean, *O. tricolor* Dejean, *O. hoepfneri* Dejean, and *O. sallei* Chaudoir.

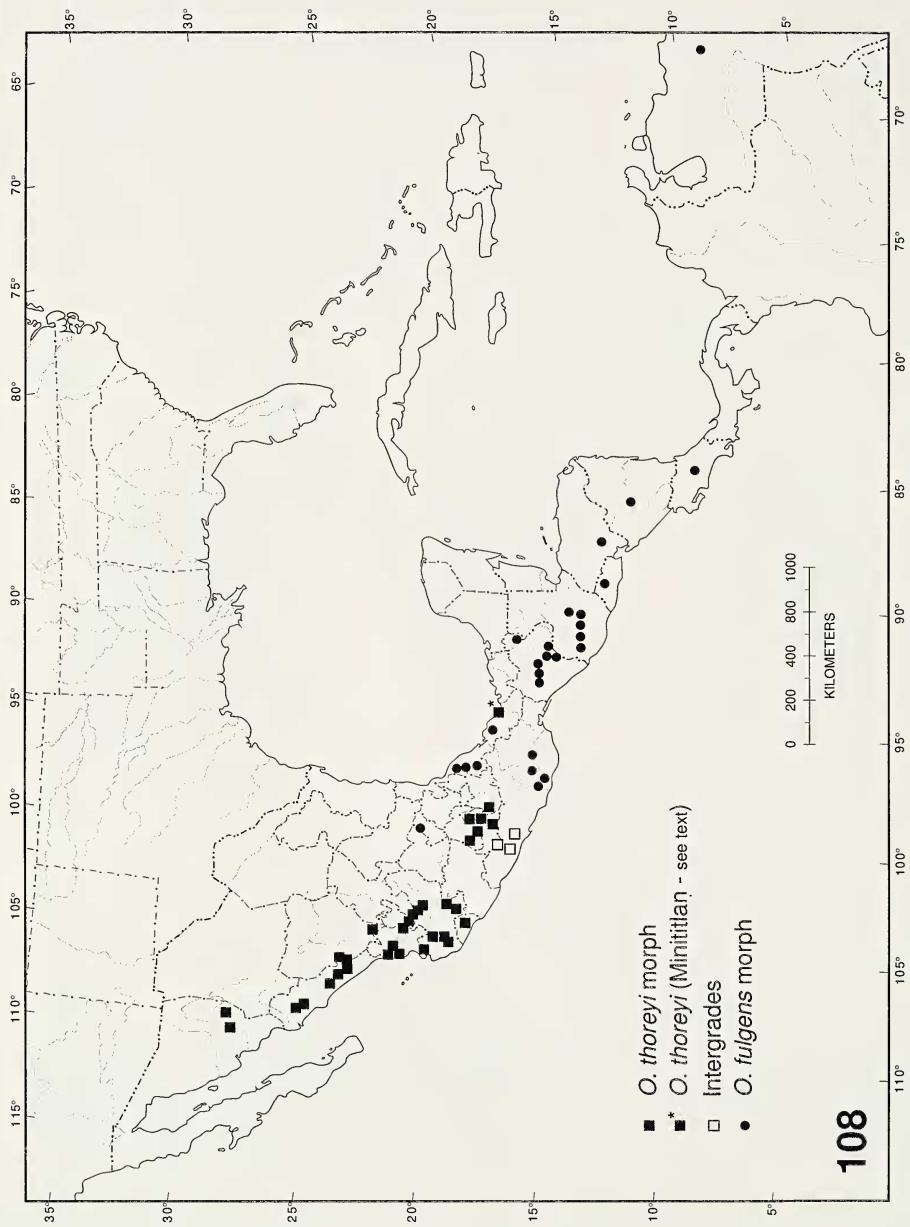


Fig. 108.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the geographical forms of *O. fulgens* Dejean; Venezuelan record excluded.

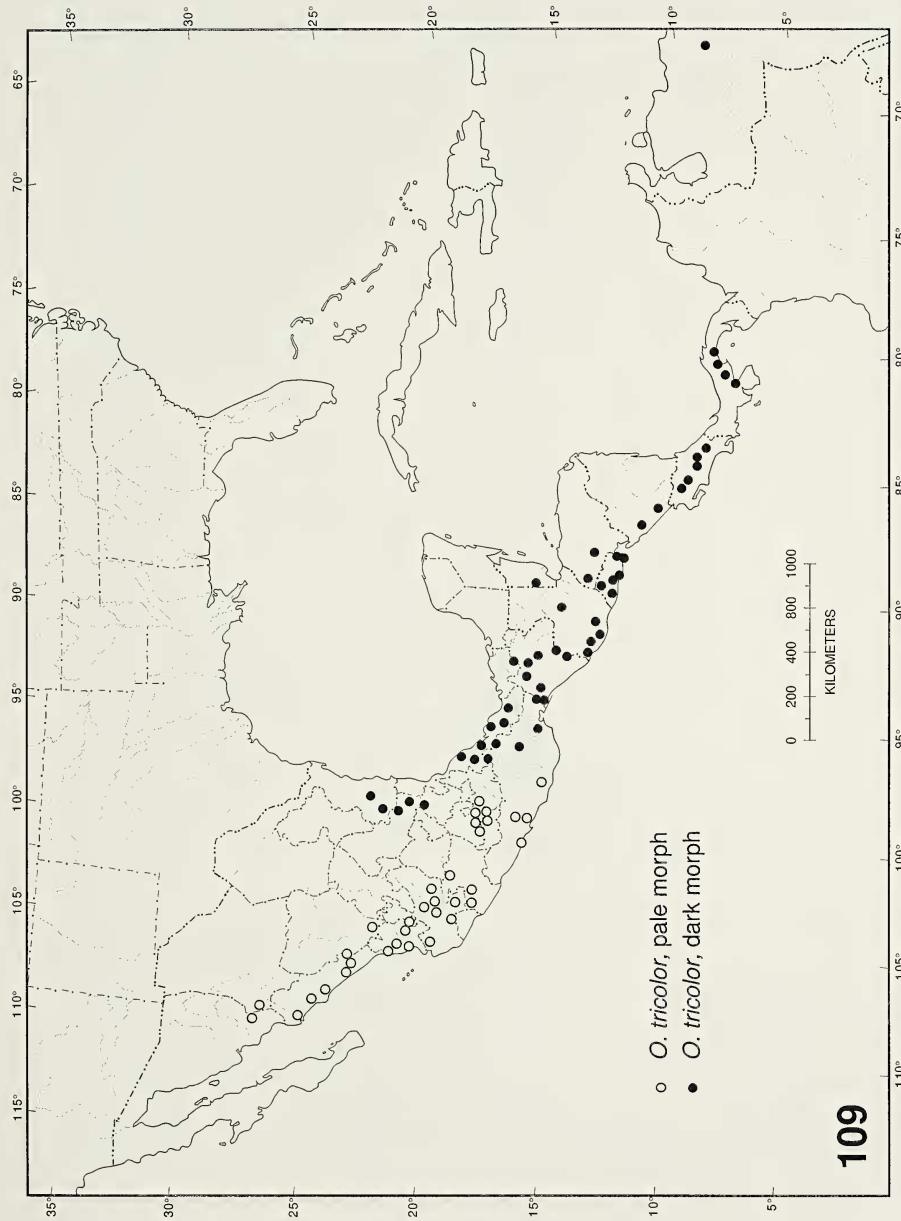


Fig. 109.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the geographical forms of *O. tricolor* Dejean; Venezuelan record excluded.

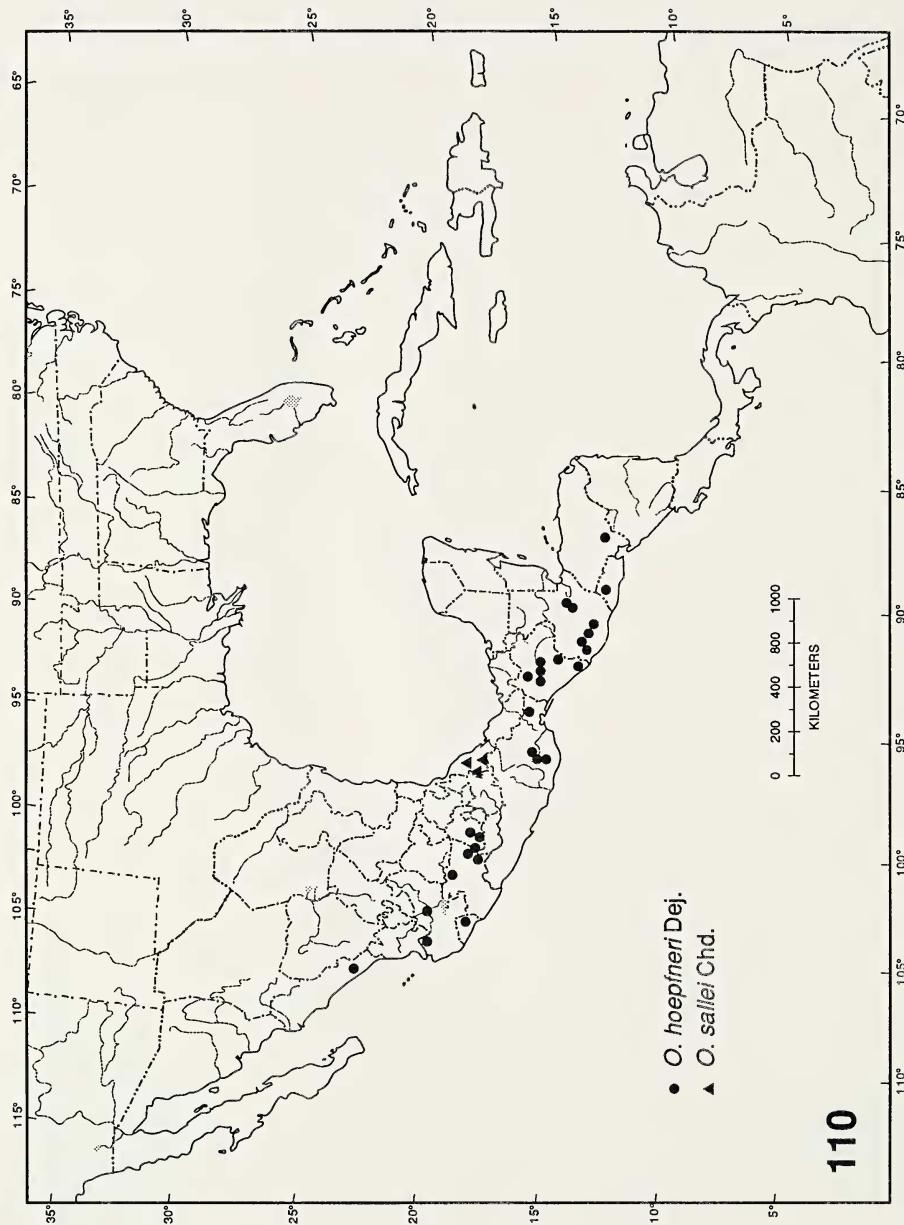


Fig. 110.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for *O. hoepfneri* Dej. and *O. sallaei* Chaudr.

Table 4.—Altitudinal ranges (*m* above sea level), based on collecting records, of the species of *Onypterygia* Dejean.

Species	Altitudinal range	Flight wing development <sup>1</sup>
<i>amecameca</i>	2400	—
<i>atoyac</i>	2300	—
<i>rubida</i>	2100–2600	+,-
<i>pacifica</i>	2000–2150	—
<i>stenapteryx</i>	1700–2200	—
<i>shpeleyi</i>	1700	—
<i>wappesi</i>	1700	—
<i>cupricauda</i>	1600–1800	+,-
<i>donato</i>	1500	—
<i>polytreta</i>	1500	+
<i>pallidipes</i>	1400–2100	+
<i>crabilli</i>	1400–1550	+
<i>chrysura</i>	1400	+
<i>pseudangustata</i>	1350–2000	+
<i>longispinis</i>	1300–1900	+
<i>aeneipennis</i>	1300–1400	—
<i>championi</i>	1300	+
<i>batesi</i>	1150–2200	+,-
<i>angustata</i>	1000–2300	+
<i>hoepfneri</i>	1000–2100	+
<i>quadrispinosa</i>	1000–1500	+
<i>kathleenae</i>	900–1900	+
<i>sallei</i>	900–1500	+
<i>pusilla</i>	850–1400	+
<i>iris</i>	800–1650	+
<i>famini</i>	700–2300	+
<i>rawlinsi</i>	700–1550	+
<i>perissostigma</i>	600	+
<i>stribungi</i>	600	+
<i>exeuros</i>	600	+
<i>fulgens</i>	0–2500	+
<i>tricolor</i>	0–2300	+
<i>cyanea</i>	0–2200	+
<i>scintillans</i>	?	+

<sup>1</sup>— = Brachypterous, wings not functional as flight organs. + = Macropterous, wings functional as flight organs.

chypterus condition of all species of the *wappesi* species group indicates an immediate ancestor that was brachypterus.

We postulate further that the *wappesi* and *aeneipennis* species groups are among the more basal (i.e., closer to ancestral *Onypterygia*) and that their present confinement to higher altitude is consistent with taxon cycle (Wilson, 1961) or taxon pulse (Erwin, 1979, 1985) theory, which predicts the restriction of ranges, and ecological amplitudes of the more ancestral taxa of lineages. In contrast, the more derived (postulated to be later-evolving) lineages of *Onypterygia* exhibit more extensive altitudinal ranges (Table 4). The species of some species pairs of adelphotaxa differ from one another in altitudinal distribution (cf. especially *O. shpeleyi*–*pacifica*, *O. pallidipes*–*rubida*, *O. rawlinsi*–*pusilla*, and *O. kathleenae*–*exeuros*), suggesting range reduction and subsequent specialization of vicars of wider-ranging ancestral stocks.

#### Habitat

Forest-associated, the ecological range of the species of *Onypterygia* extends from dry, lowland tropical forest ("Bosque Tropical Subcaducifolio," "Bosque

Tropical Caducifolio," and "Bosque Espinoso" [Rzedowski, 1978]) to higher-altitude moist to wet tropical montane forest ("Selva Alta o mediana subperennifolia" [Sarukhan, 1968]) to cloud, oak-pine, and pine-fir forests ("Bosque de coníferas y de *Quercus*" and "Bosque Mesófilo de Montaña" [Rzedowski, 1978]). Most species live in trees or low bushes and vines in montane tropical, to oak-pine forests. Evidently, the higher altitude cold fir forests have been invaded only marginally. The ecological range of two species, *O. fulgens* and *O. tricolor*, extends from tropical deciduous to at least oak-pine forests. *Onypterygia cyanea*, of the *O. famini* species group, tends to occupy and may be restricted to relatively dry forests, at lower altitudes.

Extensive range overlap is common, especially among species not very closely related. For example, during a short trip to the mountains of Guatemala, during the period May 19–June 13, 1991, six species of *Onypterygia* that represented four species groups were encountered. Eleven localities were sampled, some only at night, some during daylight.

Of these species, *O. pusilla* was represented by a single specimen, *O. tricolor* by three specimens at one locality, and *O. famini* by six specimens taken at UV light, at one locality. Three species, *O. angustata*, *O. longispinus*, and *O. fulgens*, were encountered more commonly.

Range overlap was extensive in the montane tropical and oak-pine forests. In the higher altitude, colder, oak-pine forests in the vicinity of Guatemala City, only *O. angustata* was found. Conversely, this species seemed relatively scarce at altitudes less than 1650 m, whereas another member of the *angustata* species group, *O. longispinus*, was encountered frequently at the lower altitude.

Had we collected in these localities at other times in the year, or under other climatic conditions, the results might have been different, in that the less frequently collected species may have been more common. Regardless, the relative scarcity of three of the species may be evidence of ecological differentiation within *Onypterygia*, just as the somewhat different distribution of *O. angustata* and *O. longispinus* is suggestive of ecological differentiation within one species group. Similarly, although the ranges of *O. fulgens* and *O. tricolor* overlap extensively throughout Middle America, during our time in Guatemala the former was relatively abundant and the latter very scarce.

The three common species were encountered both by night (principally at UV light) and by day. Occurrence at light suggests night flight, and thus nocturnal activity. The beetles were not seen running or flying during the day (they were taken principally by beating vegetation [green leaves] and by removing epiphytes and various types of debris associated with living trees), and may not have been active then.

### Conclusions

The limited ecological data available, especially altitudinal range, show some differences among evolutionarily significant groups of taxa (for example, at the level of species group and species pairs of adelphotaxa). We take this as evidence for ecological differentiation in the course of development of the extant assemblage of species of *Onypterygia*.

### Evolutionary Considerations

#### Structural Features

Based on the notion of a generalized member of the subtribe Platynina, to which *Onypterygia* belongs, we postulate some trends in structural features. Setae have

been lost from the pronotum and elytral disc, and have been gained, principally on abdominal sternum VII. The elytra have been modified through development of apical and sutural spination, development (and probably subsequent reduction) of a posterolateral callus, development of large pits in the discal surfaces, and foveate umbilical and discal setigerous punctures, and reduction of interneurs. Hind wings have been reduced (with consequent loss of ability to fly), and as well, the metathorax has been reduced. Tarsomeres have been modified, principally tarsomere 4, by lengthening of the outer apical lobe.

The male genitalia exhibit striking modifications, principally in size of internal sac and in its armature. Two types of armature have developed (spinose setae and setose spines), and show trends both to increased complication and loss.

Female ovipositors have been modified also, principally in form (from falcate to lobate) and in setation of stylomere 2 (from few to numerous ensiform setae, on the lateral surfaces). The reproductive tract itself evidently was modified, with potential lengthening of the bursa copulatrix, in correlation with lengthening of the male internal sac. Body colors exhibit substantial variation, by individual part and by total pattern of each species. However one interprets evolution of color, substantial homoplasy will have to be postulated.

Tarsal claws exhibit two conditions: pectinations more, or less, numerous. The latter condition characterizes one species only, *O. perissostigma*, which is enigmatic in a number of other features, too. The lower number of pectinations could represent reduction and be thereby apotypic, or could represent the original condition for *Onypterygia*, and thus be plesiotypic. We decline to make further comment now.

#### *Structural Features and the Species Groups*

The species groups are designated, rather arbitrarily, as basal or derived. More basal are the *famini*, *wappesi*, *aeneipennis*, and *pusilla* groups. The more derivative are the *angustata* and *fulgens* groups, with the most markedly derived features in the latter group. The *perissostigma* group occupies an intermediate position, although we regard it as basically primitive.

#### *Geographical History*

*Introduction.*—The known geographical ranges of the species of *Onypterygia* are basic empirical components of this analysis (Fig. 27, 33, 46, 52, 62, and 107–110). Also, a general theory of evolution of distribution patterns of Neotropical taxa is used that has been developed during the past half century by biogeographers and geologists; see, in particular, Whitehead (1976), Schreiber (1978), Erwin (1979), Noonan (1979, 1988), Savage (1982), and Halffter (1987). For zoogeographical analyses of taxa of Carabidae with ranges comparable to those of *Onypterygia*, see references in Noonan (1985) and Liebherr (1991a, 1991b, 1994).

*Distribution Patterns.*—At the generic level, the distribution pattern of *Onypterygia* is designated here as “the Meso-American Montane Pattern” of Halffter (1987:107). This is an assumption, based on the general similarity of the distribution pattern to that of the *Platynus degallieri* group (Liebherr, 1994:843). The adelphotaxon of *Onypterygia* may have been South American or Middle American in origin. As a member of the Meso-American Montane assemblage, the time of origin of *Onypterygia* is postulated reasonably as Oligocene–Miocene (Liebherr, 1992:108), or between, say, 20 and 30 million years before present.

The distribution pattern of *Onypterygia* is presented in terms of species diver-

Table 5.—Number of species of *Onypterygia* Dejean, by 5°-intervals of latitude.

Latitude	Number of species
25–30	3
20–25	6
15–20	24
10–15	14
5–10	9

sity and postulated interspecific relationships. A general synthesis is based on correlating the chorological patterns and the relationship of some of the species.

Latitudinally species number (Table 5) is minimal toward the north, with the ranges of only three species extending north of the Tropic of Cancer; the northernmost record for *O. hoepfneri* is either just slightly north of or slightly south of that line; being marginal, it was excluded from the group of species whose ranges extend farther north. Numbers are maximal in central Mexico and decrease into lower Central America. Only two species, *O. fulgens* and *O. tricolor*, are known to enter South America, and their ranges do not extend as far south as the Amazon Basin.

The ranges of about two-thirds of the species are confined to a single 5°-unit (Table 6), with a marked decrease in numbers to a single species that ranges through all five units. The longitudinal component of the distribution pattern is shown by numbers of species with ranges confined to either the Pacific Versant (16 species) or the Atlantic Versant (seven species). In summary, the distribution of *Onypterygia* is principally tropical and almost exclusively Middle American. Most species have restricted ranges, and species are more numerous on the Pacific than on the Atlantic Versant.

In his study of cladistic-biogeographic patterns of distribution of montane Middle American Carabidae, Liebherr (1994) recognized a series of "areas of endemism," based in part on geological considerations. With modifications and refinements indicated below (Table 7), these areas (Fig. 111) are used here to describe distribution patterns of the species of *Onypterygia*. The term "endemism" is replaced here with *precinctive*, a noun derived from the adjective *precinctive* (Frank and McCoy, 1990, 1995; see also Shpeley and Ball, 1994:18).

Liebherr (1994:847, fig. 4) recognized five northern areas. In the absence of northern precinctive taxa of *Onypterygia*, four of these areas are combined as the Sierra Madre Occidental. The Sierra Madre Oriental is distinguished because of its different composition of *Onypterygia* species. Liebherr's "Sierra Transvolcanica" is divided into two parts. Similarly, the "Sierra Madre del Sur" system is divided into three areas, although the collective term is used as necessary, or convenient.

Table 6.—Number of species of *Onypterygia* Dejean by number of 5°-intervals of latitude occupied.

Number of units occupied	Number of species
One	22
Two	6
Three	3
Four	2
Five	1

Table 7.—Areas of precinction (= endemism) inhabited by the species of *Onypterygia* Dejean.

Liebherr (1994) system	Present system
Arizona Mountains	
Sonoran Desert	
Sierra Madre Occidental	Sierra Madre Occidental
Sierra Madre Occidental (S)	Sierra Madre Oriental
Sierra Madre Oriental	Sierra Transvolcanica East
Sierra Transvolcanica	Sierra Transvolcanica West
Sierra Madre del Sur	Sierra Madre de Oaxaca
Chiapan-Guatemalan Highlands	Sierra de Atoyac
Talamancan Cordillera	Sierra de Miahuatlán
	Chiapan-Guatemalan Highlands
	Talamancan Cordillera

Based on Binford (1989:352, fig. 31), the Sierra Madre de Oaxaca includes the Sierra de Juárez, the Sierra Aloapaneca, and the Sierra de Zempoaltepec; and "Sierra de Atoyac" is used for that part of the Sierra Madre del Sur located in the state of Guerrero. For convenience, the term "Sierra de Miahuatlán" is used to include that range as well as the Sierra Yucuyácu and the Sierra de Cuatro Venados, all three ranges being in the Pacific drainage systems of Oaxaca, in contrast to the Atlantic drainage system, in which the Sierra Madre de Oaxaca is located. These modifications are based on the restricted known ranges of many of the species of *Onypterygia*. The "Chiapan-Guatemalan Highlands" and "Talamancan Cordillera" are accepted as delimited by Liebherr.

Group occupancy ranges from one (*perissostigma* species group—Sierra de Juárez, in the Sierra Madre de Oaxaca) to all nine areas of precinction, with most groups occupying at least six areas (Table 8). The *fulgens* group has representative taxa in all areas. Most areas of precinction have from four to six of the seven species groups of *Onypterygia*. The Sierra Madre de Oaxaca and the Sierra Transvolcanica West have the most species groups, while the Sierra Madre Occidental and Talamancan Cordillera have the least.

The species of the more basal lineages (Subtotal A) are concentrated in the Sierra Transvolcanica West and Sierra de Atoyac, whereas the species of the more derived lineages (Subtotal B) are more numerous in the Chiapan-Guatemalan Highlands and Talamancan Cordillera (Tables 9–11). The northern areas (Sierra Madre Occidental, Sierra Madre Oriental) are without precinctive species. The Talamancan Cordillera has the largest number (five), followed by the Sierra Transvolcanica West and the Sierra Madre de Oaxaca, with four each. Generalizing the pattern by combining with themselves the parts of the Sierra Transvolcanica and the Sierra Madre del Sur, the pattern of precinction from northern Mexico to Panama is: 0–6–9–1–5. This illustrates the numerical preponderance of the Sierra Madre del Sur (with nine precinctive species), followed by that of the Sierra Transvolcanica (six precinctives). Most species (22) are known from (and possibly confined to) single areas of precinction (Table 12). Only two species are known from all areas. Eleven species are represented in two to seven areas of precinction.

Lowlands separate the adjacent areas of precinction from one another. These are regarded as topographical barriers that restrict the movements of taxa occupying the areas of precinction (Fig. 111). The Isthmus of Tehuantepec, for purposes of analysis, is treated as two barriers, one for the Pacific Versant and one

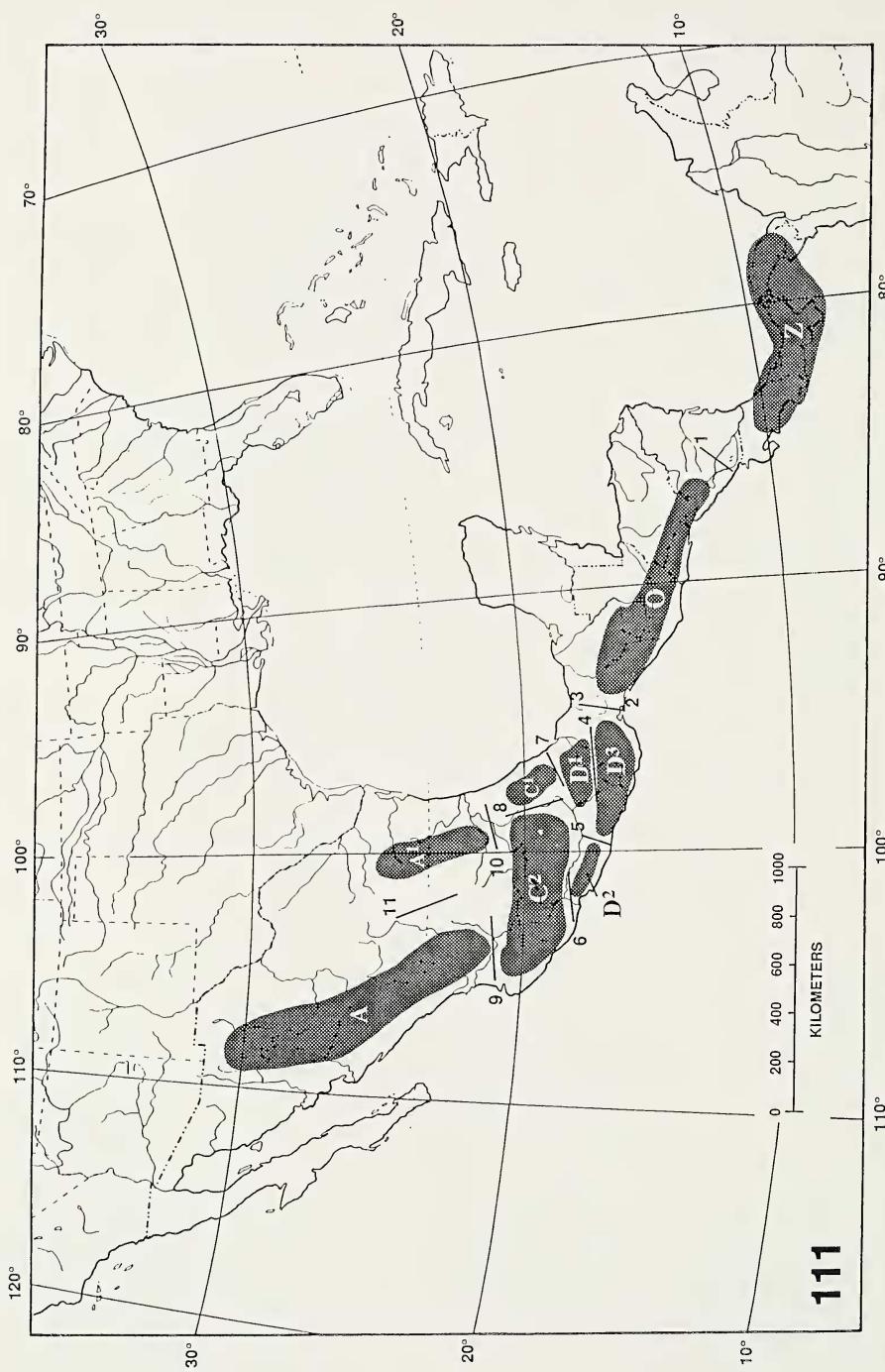


Fig. 111.—Map of southern North America, Middle, and northern South America, showing positions of Middle American areas of precipitation modified from Liebherr (1994), and the postulated topographical barriers (represented by numbered lines) between adjacent areas. See text for further details. Legend: A, Sierra Madre Occidental; C<sup>1</sup>, Sierra Transvolcanica East; C<sup>2</sup>, Sierra Transvolcanica West; D<sup>1</sup>, Sierra Madre Oriental; D<sup>2</sup>, Sierra de Atoya; D<sup>3</sup>, Sierra de Miahuatlán; O, Chiapan-Guatemalan Cordillera; Z, Talamancan Highlands.

Table 8.—Distribution of the species groups of *Onypterygia Dejean* in relation to areas of precinction.

Areas of precinction	Species group <sup>1</sup>						Total number groups/area
	per	wap	aen	fam	pus	ang	
Sierra Madre Occidental				X		X	2
Sierra Madre Oriental			X	X	X	X	5
Sierra Transvolcanica East			X	X	X	X	5
Sierra Transvolcanica West	X		X	X	X	X	6
Sierra Madre de Oaxaca	X		X	X	X	X	6
Sierra de Atoyac		X	X	X	X	X	5
Sierra de Miahuatlán		X	X	X	X	X	6
Chiapan-Guatemalan Highlands				X	X	X	4
Talamancan Cordillera						X	X
Total areas occupied/group	1	3	6	8	7	7	9

<sup>1</sup> Abbreviations of names of species groups: *aen*, *aeneipennis*; *ang*, *angustata*; *fam*, *famini*; *ful*, *fulgens*; *per*, *perissostigma*; *pus*, *pusilla*; and *wap*, *wappesi*.

for the Gulf Versant. Twelve species have crossed one or more of these barriers, probably in Recent time (Table 13).

No species have crossed the Mexican Plateau north of the Sierra Transvolcanica (Barrier No. 11), and relatively few species have crossed the Nicaraguan Depression (Barrier No. 1), supporting Halffter's (1987:107) assessment (Table 13). In contrast, Barrier No. 10 (the lowlands and low mountains between the Sierra Madre Oriental area of precinction and the Sierra Transvolcanica East) has been crossed by most of the extant species of *Onypterygia* in the region.

The Isthmus of Tehuantepec (Barrier 2–3) has been crossed relatively frequently, as one might expect from Halffter's (1987:108) estimate of the strength of this barrier for tropical-adapted species. In the past, the situation might have been quite different, with so much of the evolution of the *fulgens* species group having occurred to the southeast of this barrier.

Although the species *O. fulgens* and *O. tricolor* are both widespread, their geographical differentiation (Fig. 108, 109) may be viewed as evidence that their extensive ranges developed in pre-Recent (probably Pleistocene) time, and were separated into northwestern and southeastern vicariads leading to infraspecific differentiation. Because of the extensive ranges of these two species, the putative refugia of the infraspecific morphs cannot be estimated.

*Evolutionary Correlations.*—These correlations are sought for both species groups and species. The more derived, or younger groups are the more widespread (Table 8), just as many of the more structurally derived species are the most widespread (Table 10). The older species groups are concentrated in the Sierra Transvolcanica and the Sierra Madre del Sur, whereas the more recent groups are best represented in the more southern precinctive centers.

Seven pairs of species-level adelphotaxa exhibit allopatric patterns (Table 14). One pair (*pallidipes*–*rubida*) has differentiated within a single area of precinction (Sierra Transvolcanica West). For the remaining six pairs, one can infer differentiation between areas of precinction, or if within, then between different parts of that area: *championi*–*donato* and *polytreta*–*crabilli*, different parts of the Talamancan Cordillera; *shpeleyi*–*pacifica*, Sierra de Atoyac and Sierra de Miahuatlán; *hoepfneri*–*sallei*, Sierra Transvolcanica East and West; and *pseudangustata*–*striblingi*, Sierra Transvolcanica East and Sierra Madre de Oaxaca. Differentiation of the species pair *pusilla*–*rawlinsi* may have occurred within the Sierra Transvol-

Table 9.—Distribution of the species of the *perissostigma*, *wappesi*, *aeneipennis*, *famini*, and *pusilla* species groups of *Onypterygia Dejean*, in relation to areas of precinctation.

Areas of precinction	Species <sup>1</sup>												Subtotal A species/area				
	per	wap	ame	ato	shp	puc	bat	aen	cup	ste	pal	rub	fam	cya	raw	pus	
Sierra Madre Occidental							X					X	X				1
Sierra Madre Oriental							X					X		X			3
Sierra Transvolcanica East							X			X		X	X				3
Sierra Transvolcanica West							X			X		X	X				9
Sierra Madre de Oaxaca	X		X				X			X		X	X				4
Sierra de Atoyac		X		X	X				X		X	X	X				7
Sierra de Miahuatlán												X	X				4
Chiapan-Guatemalan Highlands								X				X		X			2
Talamancan Cordillera												X		X			
Subtotal A																	
Number of areas occupied/species	1	1	1	1	1	1	4	1	1	1	1	1	1	1	1	1	7

<sup>1</sup> Abbreviations of specific epithets: *aen*, *aeneipennis*; *ame*, *amecanea*; *ato*, *atoyac*; *bat*, *batesi*; *cup*, *cupricauda*; *cya*, *cupricauda*; *fam*, *famini*; *pac*, *pacifica*; *pal*, *pallidipes*; *per*, *perissostigma*; *pus*, *pusilla*; *raw*, *rawlinii*; *rub*, *rubida*; *shp*, *shpeleyi*; *ste*, *stenapteryx*; and *wap*, *wappesi*.

Table 10.—Distribution of the species of the *angustata* and *fulgens* species groups of *Onypterygia Dejean*, in relation to areas of precinctio.

Areas of precinctio	Species <sup>1</sup>												Subtotal B species/area						
	lon	ang	pse	str	iri	cha	don	chr	kar	exe	pol	cra	qua	sci	ful	tri	hoe	sal	
Sierra Madre Occidental		X													X	X	X	X	3
Sierra Madre Oriental		X	X		X										X	X	X	X	3
Sierra Transvolcanica East		X													X	X	X	X	6
Sierra Transvolcanica West		X													X	X	X	X	4
Sierra Madre de Oaxaca				X					X	X					X	X	X	X	6
Sierra de Atoyac															X	X	X	X	3
Sierra de Miahuatlán		X				X			X	X					X	X	X	X	4
Chapán-Guatemalan Highlands	X	X				X			X	X					X	X	X	X	9
Talamancan Cordillera	X					X	X					X	X		X	X	X	X	10
Subtotal B																			
Number of areas occupied/species	1	6	1	1	2	1	1	2	2	1	1	1	2	1	1	9	9	6	1

<sup>1</sup> Abbreviations of specific epithets: *ang*, *angustata*; *cha*, *championi*; *chr*, *chrysura*; *cra*, *crabili*; *don*, *donato*; *exe*, *exeuropis*; *hoe*, *hoeppfieri*; *iri*, *iris*; *lon*, *longispinis*; *kar*, *kathleenae*; *pse*, *pseudoleanae*; *pol*, *pseudangustata*; *qua*, *quadrispinosa*; *sal*, *sallei*; *sci*, *scimillans*; *sur*, *stribilingi*; and *tri*, *tricolor*.

Table 11.—Total number of species of *Onypterygia* per area of precintion. Data derived from tables 9 and 10.

Areas of precintion	Number of species		
	Subtotal A	Subtotal B	A + B
Sierra Madre Occidental	1	3	4
Sierra Madre Oriental	3	3	6
Sierra Transvolcanica East	3	6	9
Sierra Transvolcanica West	9	4	13
Sierra Madre de Oaxaca	4	6	10
Sierra de Atoyac	7	3	10
Sierra de Miahuatlán	4	4	8
Chiapan-Guatemalan Highlands	2	9	11
Talamancan Cordillera	0	10	10

canica West, where both species are represented, or between the latter and one of the other areas in which *O. pusilla* is represented, but not *O. rawlinsi*.

One species pair (*famini*—*cyanæa*) exhibits a parapatric distribution pattern, with the ranges of both species in contact or nearly so, in the Sierra Madre de Oaxaca and Sierra Transvolcanica West. However, *O. cyanæa* occupies drier areas than those occupied by *O. famini*. Also, the range overlap is not total, each species occupying different areas in the northern parts of their respective ranges.

Three species pairs are at least partly sympatric, with overlapping ranges in the Sierra Madre de Oaxaca (*kathleenae*—*exeuros*), or the Talamancan Cordillera (*championi*—*donato*, *quadrispinosa*—*scintillans*).

One set of six species (the *aeneipennis* species group) involves principally allopatric and parapatric affinities, with partial sympatry among the older members; and one set of four species (*longispinis*—*angustata*—*pseudangustata* + *striblingi*) involves principally allopatry, with partial sympatry exhibited by the two older species. In only one species group (*fulgens*) is sympatry extensive.

In summary, allopatry, parapatry, or partial sympatry are the dominant types of distribution patterns among the more closely related species of *Onypterygia*. Among the more distantly related (i.e., those that are less similar to one another in structural features) species and species groups, more or less extensive sympathy is the rule.

*Area Affinities*.—In general, the distribution patterns of the moderately widespread species and older (more basal) species groups (Table 9) indicate a close

Table 12.—Number of species of *Onypterygia Dejean* in relation to number of areas of precintion occupied. Data derived from tables 9 and 10.

Number of areas of precintion occupied	Number of species
One	22
Two	4
Three	1
Four	1
Five	0
Six	2
Seven	2
Eight	0
Nine	2

Table 13.—Distribution of wider-ranging species of *Onypterygia Dejean*, in relation to crossed topographical barriers between adjacent areas of precipitation. The number of barriers crossed is expressed as a percentage of the total number of species (less those known from a single locality, only) that occur on each side of the barrier in adjacent areas of precipitation. Each percentage is accepted as representing roughly the relative strength of the barrier in question.

Species	Barrier number <sup>1</sup>										Total number of barriers crossed
	11	9	1	8	6	4	3	5	7	2	
<i>chrysura</i>	X										1
<i>quadrispinosa</i>	X										1
<i>iris</i>											2
<i>kathleenae</i>											2
<i>batesi</i>	X	X	X	X	X	X	X	X	X		
<i>cyannea</i>											2
<i>angustata</i>											5
<i>hoepfneri</i>	X										6
<i>famini</i>											7
<i>pusilla</i>	X	X	X	X	X	X	X	X	X		8
<i>fulgens</i>											10
<i>tricolor</i>	X	X	X	X	X	X	X	X	X		10
Total number of species crossing	0	4	5	5	6	6	6	5	6	8	5
Total species available <sup>2</sup>	6	9	11	10	12	11	11	9	11	13	7
% total available species crossing barrier	0	44	45	50	50	54	54	56	54	61	71

<sup>1</sup> For positions of barriers, see Fig. 111.

<sup>2</sup> Total number of species adjacent to barrier.

Table 14.—*Species-level adelphotaxa of Onypterygia Dejean and their chorological affinities.*

Figure number	Species pairs	Geographic association		Putative barriers or areas of contact
		Parapatric	Allotopic	
33	<i>shapeleyi</i> — <i>pacifica</i>		X	between D <sup>2</sup> and D <sup>3</sup> (barrier number 5)
27	<i>famini</i> — <i>cyanaea</i>	X		between C <sup>1</sup> and C <sup>2</sup> (barrier number 8) within D <sup>3</sup>
110	<i>hoepfneri</i> — <i>sallei</i>	X		between C <sup>1</sup> and C <sup>2</sup> (barrier number 8)
62	<i>pseudangustata</i> — <i>striplingi</i>	X		between C <sup>1</sup> and D <sup>1</sup> (barrier number 7)
52	<i>rawlinsi</i> — <i>pusilla</i>	X		within C <sup>2</sup>
46	<i>pallidipes</i> — <i>rubida</i>	X		within D <sup>1</sup>
107	<i>kathleenae</i> — <i>exeuros</i>	X		within Z
107	<i>quadrispinosa</i> — <i>scintillans</i>	X		within Z (secondary overlap)
107	<i>championi</i> — <i>donato</i>	X		within Z
107	<i>polymera</i> — <i>crabilli</i>	X		

affinity between the adjacent Sierra Transvolcanica and Sierra Madre del Sur. Similarly, the distribution patterns of pairs of adelphotaxa (Table 14) indicate a marked affinity between the Chiapan-Guatemalan Highlands and the Talamancan Cordillera. The *famini* and *pusilla* species groups indicate an affinity among the Transvolcanic, Oaxacan, and Chiapan-Guatemalan areas of precintion, and places the Talamancan area in isolation. In contrast, marked affinity is exhibited between the Chiapan-Guatemalan Highlands and the Talamancan Cordillera by the concentration therein of the *fulgens* group in general, and in particular by the species-pair *quadrispinosa*-*scintillans*, and the triad *iris*-*championi* + *donato*. For the northern areas, the distribution of species groups indicates a closer affinity between the Sierra Madre Oriental area and the southern areas than between the latter and the Sierra Madre Occidental. The overall pattern is indicative of concentration of seemingly older centers of differentiation in the Sierra Transvolcanica and Sierra Madre del Sur, with a more recent center in the Talamancan Cordillera. Also indicated is continued differentiation in the older centers, leading in them to a combination of comparatively recently evolved species and older lineages.

*Chorological Scenario*.—The data about geographical distribution of the species of *Onypterygia* suggest cyclic vicariance (Noonan, 1988:377–378). As formulated by Ball and Nimmo (1983:344–345) this hypothesis is based on a postulated sequence of alternating periods of favorable and unfavorable climates (or other circumstances), with resident taxa being alternatingly widespread during favorable periods, and with restricted ranges during unfavorable periods. Restricted areas for survival during unfavorable periods are refugia; these persist, to function again and again as survival centers. During unfavorable periods, the ranges of taxa are fragmented into isolated vicarages provided by the refugia, and in isolation the resulting vicars undergo differentiation that can lead to speciation. During favorable periods, the taxa become widespread by dispersal, with consequent increase in diversity in areas of overlap of previously isolated groups. This hypothesis was used by Peck (1973:150–156, note especially fig. 216) to explain evolution of the Appalachian species of *Adelops*, and is applicable to the distribution patterns of a variety of Neotropical taxa (see, for example, Haffer, 1982:9).

Applied specifically to *Onypterygia*, mesic montane tropical forests at 1000 to 1500 m altitude are interpreted as the refugial areas for the species. The lower slopes were invaded and lowland intermontane barriers likely were crossed during especially favorable (with more rainfall?) climatic periods.

The early evolution of species groups likely was concentrated to the north of the Isthmus of Tehuantepec because the ranges of the more basal stocks are concentrated there. Possibly in late Miocene–early Pliocene time, that barrier (No. 2–3, Fig. 111) was crossed by one lineage of *Onypterygia* that spread southeastward, entering the Chiapan-Guatemalan Highland system and Talamancan Cordillera (across the Nicaraguan Depression—Barrier No. 1), and differentiating to form the *angustata* and *fulgens* species groups. That differentiation might have involved two vicariance events: one, between the Oaxaca mountains and the more southern ranges, and the second, between the Chiapan-Guatemalan Highlands and the Talamancan Cordillera. Invasion of the latter mountain system might not have taken place until Pliocene time, with formation of land connections between nuclear and lower Central America.

Continued climatic fluctuations through Late Tertiary and Quaternary time influenced the ebb and flow of the *Onypterygia* populations and their differentiation.

Under ecologically favorable conditions, species were more widespread; under unfavorable conditions, they were restricted to montane refugia, when differentiation of formerly conspecific vicars took place. The most recent events, probably, were the invasion of the western slopes of the northern Sierra Madre Occidental by species of the *famini* and *fulgens* groups, and the invasion of northern South America by at least two species of the latter group only. Preceding these invasions, both *O. fulgens* and *O. tricolor* had differentiated partially, each represented by a pair of geographically distinctive morphs.

Although range restriction alternating with expansion provides the physical basis for development of diversity overall, the system does not account for continued restriction of species to single mountain systems. Only those taxa become widespread that have the adaptations to use the favorable conditions to enter the lowlands. The species *O. fulgens* and *O. tricolor*, for example, evidently had the necessary adaptations, and became very widespread, although probably over an extended period involving more than one cycle of favorable–unfavorable conditions. This is shown by the marked intraspecific differentiation exhibited by each of them, that probably developed during an isolation phase that preceded the Holocene Epoch.

In contrast, the members of the *wappesi* and *aeneipennis* species groups probably are becoming bound to montane habitats, as shown by wing loss and seeming restriction to higher altitudes. This does not preclude intramontane differentiation within a single mountain system or massif.

#### CONCLUSION

Some 166 years have elapsed since *Onypterygia* was named as a genus of Carabidae by P. F. M. A. Dejean, and it is 117 years since the genus was last revised by Maximilien de Chaudoir. Henry Walter Bates, some 113 years ago, placed those species plus additional species that he discovered in the general context of the Middle American insect fauna, as he knew it. The present contribution has focused on making known the work of these illustrious predecessors, and placing it in the context of what new knowledge we have been able to acquire, thanks to the efforts of many colleagues, as well as our own explorations, in Mexico.

We have provided also the beginning of a basis in evolutionary theory for further study of the species. This framework should be adequate for integrating the work that must be undertaken to achieve yet another more advanced level of understanding: details about distribution, in terms of ecological features, such as: altitudinal range and association with forest types; activity patterns and other aspects of life history; and geographical range, particularly in relation to the postulated areas of precintion (too many species of *Onypterygia* are known from single localities only). Additional character systems ought to prove enlightening: setal patterns and other aspects of larvae and pupae, and molecular data. We hope that this contribution, in the light of the additional knowledge required, will be seen as a step forward by those who follow us, in relation to the level of understanding that was achieved by those whom we have followed.

#### ACKNOWLEDGMENTS

We thank the curators of institutional collections and owners of private collections whose names are listed in the "Materials" section above, who made it possible for us to borrow and study the

specimens on which this revision is based. We note with special appreciation M. J. D. Brendell's (BMNH) assistance, and the assistance of the curators of the Hope Museum, Oxford University; The Natural History Museum, London; and the Museum National d'Histoire Naturelle, Paris (in Oxford, E. Taylor; in London, R. D. Pope, N. E. Stork, P. M. Hammond, M. E. Bacchus, and M. J. D. Brendell; and in Paris, A. Bons, J.-J. Menier, and H. Perrin).

Technical assistance was provided by several members of the Department of Entomology, University of Alberta. D. Shpeley prepared the material for study with the scanning electron microscope and associated sclerites dissected by the senior author with specimens from which they had been removed. G. B. Braybrook prepared the SEM photographs. J. S. Scott prepared the photograph that serves as Figure 1 as well as the tables, maps, and plates. Many of the line drawings were prepared by Diane Hollingdale of Edmonton, Alberta.

Alfred F. Newton (Field Museum of Natural History, Chicago, Illinois) provided on short notice important information about vegetation classification in Mexico. J. E. Rawlins (Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania) assisted greatly with information on specimens and preparation of an earlier version of the manuscript. The final version was prepared with the advice and assistance of several reviewers, and editors Bradley C. Livezey and Mary Ann Schmidt.

Staff members of the Systematic Entomology Laboratory, U. S. Department of Agriculture, Agricultural Research Services, were extremely helpful in finding and assembling all of the material of *Onypterygia* in the senior author's possession at the time of his death, as well as the partially prepared manuscript and associated notes that were required to complete the task. The junior author thanks particularly R. D. Gordon, C. R. Thompson, and J. Pakaluk. D. R. Miller, head of the laboratory during Don Whitehead's later years, granted permission to release to the junior author the wherewithal to complete the work.

Grateful acknowledgment is extended to our friends who were (or are) residents of Mexico, and who helped us as we were finding our way through the country in the early months of collecting that led to this revision: Frank Harrison (deceased, Rancho del Cielo), John Hunter (deceased, Brownsville, Texas), Jorge Hendrichs, Candido Bolivar, and Padre Bernardo Rotger (all three deceased, Mexico City), Jerzy Rzedowski (Mexico City), Dennis Breedlove, (formerly of the California Academy of Sciences, San Francisco, California), and Henryce and the late William Kauffman (San Cristóbal de las Casas), Jan, and the late Harry and Rebecca Little (Lacandon forest, Chiapas).

Field work and study of type material were supported through grants from the National Science Foundation (GB 3312) and from the Natural Sciences and Engineering Research Council of Canada (A-1399) to the junior author.

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## APPENDIX

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